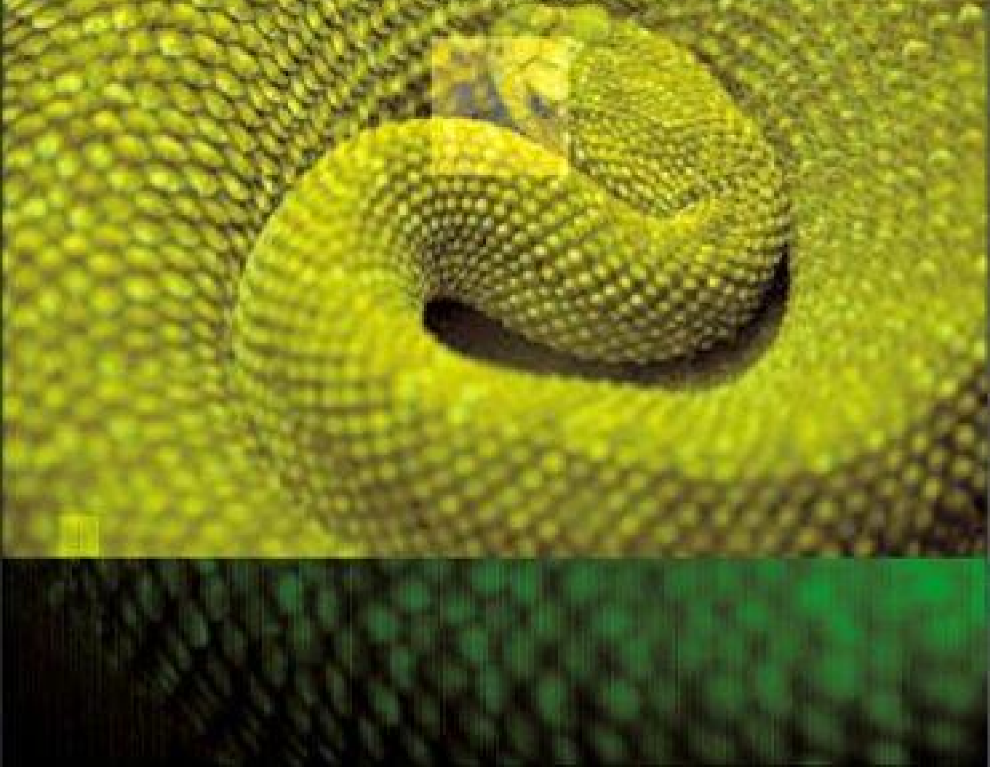
ELSEVIER
SAUNDERS

B. O'MALLEY

CLINICAL ANATOMY AND PHYSIOLOGY OF EXOTIC SPECIES:

Structure and function of mamals, birds, reptiles and amphibians



VISIT…

LANZAROTE Caliente.COM

ELSEVIER
SAUNDERS
An imprint of Elsevier Limited

© 2005, Elsevier Limited. All rights reserved.

No part of this publication may be reproduced, stored in a retrieval system, or transmitted in any form or by any means, electronic, mechanical, photocopying, recording or otherwise, without either the prior permission of the publishers or a licence permitting restricted copying in the United Kingdom issued by the Copyright Licensing Agency, 90 Tottenham Court Road, London W1T 4LP. Permissions may be sought directly from Elsevier's Health Sciences Rights Department in Philadelphia, USA: phone: (+1) 215 238 7869, fax: (+1) 215 238 2239, e-mail: healthpermissions@elsevier.com. You may also complete your request on-line via the Elsevier Science homepage (http://www.elsevier.com), by selecting 'Customer Support' and then 'Obtaining Permissions'.

First published 2005

ISBN 0 7020 2782 0

British Library Cataloguing in Publication Data
A catalogue record for this book is available from the British Library

Library of Congress Cataloguing in Publication Data
A catalog record for the book is available from the Library of Congress

Knowledge and best practice in this field is are constantly changing. As new research and experience broaden our knowledge, changes in practice, treatment and drug therapy may become necessary or appropriate. Readers are advised to check the most current information provided (i) on procedures featured or (ii) by the manufacturer of each product to be administered, to verify the recommended dose or formula, the method and duration of administration, and contraindications. It is the responsibility of the practitioner, relying on their own experience and knowledge of the patient, to make diagnoses, the determine dosages and the best treatment for each individual patient, and to take all appropriate safety precautions. To the fullest extent of the law, neither the publisher nor the author assumes any liability for any injury and/or damage.

The Publisher

Printed in Germany

The
publisher's
policy is to use
paper manufactured
from sustainable forests

Working together to grow
libraries in developing countries

www.elsevier.com | www.bookaid.org | www.sabre.org

ELSEVIER BOOK AID International Sabre Foundation

Contributors

Chapter 1 Amphibian anatomy and physiology

Peter Helmer DVM
Avian Animal Hospital of Bardmoor, Largo, Florida, USA

and

Douglas P Whiteside DVM DVSc
Staff Veterinary, Calgary Zoo, Alberta, Canada

Chapter 12 Ferrets

John H Lewington BvetMed MRCVS
Member Australian Veterinary Association (AVA) and Australian Small Animal Veterinary Association (ASDAVA), member of American Ferret Association (AFA), World Ferret Union (WFU), South Australian Ferret Association (SAFA), New South Wales Ferret Welfare Society (NSWFWS), Ferrets Southern District Perth (FSDP)

Preface

One of the main pleasures I have in working with exotic species is the fascinating diversity among my patients. Daily in practice I see living evolution from frogs to snakes to birds and small mammals. Each one presents a clinical challenge whether it is saving a tortoise found drowning in a pond, treating a parrot with sinusitis or an anorexic rabbit. Yet we really need to understand the basics – how reptiles breathe, the structure of the psittacine sinuses and the complex gastro-intestinal physiology of the rabbit – before we can properly treat these unique pets.

The internal structure and function of exotic species has always intrigued me, yet the topic was traditionally not taught at Veterinary College. I wrote this book with the intention of both redressing this balance and answering the many questions, which interest those who work with exotics. Why, for example, don't birds' ears pop when they fly, why are rabbits obligate nose breathers and how can a lizard drop its tail and grow a new one?

Over the last ten years veterinary knowledge of the medicine and surgery of exotic animals has rapidly expanded yet the basic structure and function of these diverse species have never been drawn together in a single text. With the increasing numbers of exotic pets, veterinary surgeons are at a considerable disadvantage trying to treat sick reptile, avian and rodent patients without having in-depth knowledge of the normal *bare bones* beneath.

This book, written by vets for vets, aims to merge the wealth of zoological research with veterinary medicine – bringing the reader from the dissection table into the realms of clinical practice and living patients. To this end, I have included clinical notes where applicable and items of general interest about many species.

I hope this book will inspire vets in practice, veterinary students, nurses and technicians to study this long neglected yet captivating subject and help them apply this knowledge clinically to their patients.

Acknowledgments

In writing this book I am grateful to veterinary surgeons Peter Helmer, Doug Whiteside and John Lewington for contributing the excellent Amphibian and Ferret chapters.

I would like to thank the Natural History Museum of Ireland who provided the sources for the following illustrations: Fig 6.1, 6.2, 6.5, 6.12, 6.14, 6.15, 6.17, 6.25, 6.67, 9.6, and 11.7. Also Janet Saad for her exceptional snake photographs.

The Elsevier editorial team were wonderful with their belief in this project, their constant support and endless patience. I would also like to thank Samantha Elmhurst for her skilful and beautiful illustrations. And Tasha my poor dog who missed out on walks so this book could be researched and written.

Lastly, I would like to dedicate this book to my beloved mother, the late Mary Pat O'Malley, whose enthusiasm and encouragement kept me going as I endeavoured to juggle the demands of lecturing and running my own exotic animal practice with writing this book.

1

Amphibian anatomy and physiology

Peter J. Helmer and Douglas P. Whiteside

INTRODUCTION

With over 4000 species described, the class Amphibia represents a significant contribution to the diversity of vertebrate life on earth. Amphibians occupy an important ecological niche in which energy is transferred from their major prey item, invertebrates, to their predators, primarily reptiles and fish (Stebbins & Cohen 1995).

The first amphibian fossils date back approximately 350 million years. Current evidence indicates that they descended from a group of fish similar to the coelacanth (*Latimeria chalumnae*) (Boutilier et al. 1992; Wallace et al. 1991). These fish had functional lungs and bony, lobed fins that supported the body. Further refinements of these features allowed amphibians to be the first group of vertebrates to take on a terrestrial existence. The class name Amphibia (derived from the Greek roots *amphi*, meaning "both," and *bios*, translated as "life"), refers to the dual stages of life: aquatic and terrestrial.

Multiple features support the role of amphibians as an evolutionary step between fish and reptiles. The 3-chambered heart represents an intermediary between the 2-chambered piscine model and the more advanced 3-chambered heart of the reptiles.

The trend toward terrestrial life is also evident in the respiratory system. Most species have aquatic larval forms where gas exchange occurs in external gills. Metamorphosis to the adult, usually a terrestrial form, results in the development of lungs. These primitive lungs are relatively inefficient compared to those of other terrestrial vertebrates, and respiration is supplemented by gas exchange across the skin. Secretions of the highly glandular skin help to maintain a moist exchange surface; however, amphibians are restricted to damp habitats.

Most amphibians are oviparous, similar to fish and most reptiles. Though their eggs must not be laid in completely aquatic environments, the ova lack the water-resistant membranes or shell of reptiles and birds, thus they must be deposited in very damp places to avoid desiccation.

The larval stages rely on fins to move through their aquatic environment, in a manner similar to fish. Metamorphosis includes the development of legs for terrestrial locomotion (Figs. 1.1–1.6). The dual life cycle remains evident as the limbs of many amphibians remain adapted, for instance with webbing between the toes, for aquatic locomotion.

TAXONOMY

Amphibians are classified into three orders (Table 1.1):

1. Anura (Salientia) – the frogs and toads
2. Caudata (Urodela) – the salamanders, newts, and sirens
3. Gymnophiona (Apoda) – the caecilians

Anura

By far, the Anura represent the greatest diversity of amphibians, with over 3500 living species divided among 21 families. Anura comes from the Greek, meaning "without a tail," and with the exception of the tailed frogs (Leiopelmatidae), the remainder of anurans have either a very poorly developed tail or lack one (Fig. 1.7). The larvae are unlike the adults, and lack teeth. Neoteny, the condition in which animals become able to reproduce while arrested developmentally in the larval stage (Wallace et al. 1991), is not present. The anuran families are listed in Table 1.2 (Frank & Ramus 1995; Goin et al. 1978; Mitchell et al. 1988; Wright 1996, 2001b).

Caudata

The order Caudata comprises nine families, with around 375 species described (Table 1.3). Urodeles have a long tail, with the toothed larval forms often being similar in appearance to the adults. Neoteny is common among the salamander families, with the axolotl (*Ambystoma mexicanum*) (Fig. 1.8) being the most common example (Frank & Ramus 1995; Goin et al. 1978; Mitchell et al. 1988; Wright 1996, 2001b).

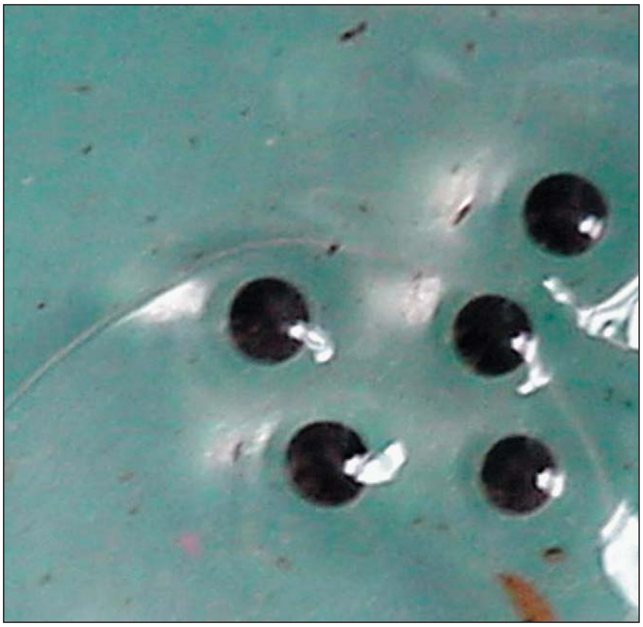


Figure 1.1 • Egg mass of Dyeing poison frog *Dendrobates tinctorius*. (Photo by Helmer.)

Gymnophiona

Although there are approximately 160 known species of caecilians, which are classified into six families (Table 1.4), clinicians will likely see them only on a sporadic basis. They are limbless, with elongate worm-like bodies, and short or absent tails (Frank & Ramus 1995; Goin et al. 1978; Mitchell et al. 1988; Wright 1996, 2001b).

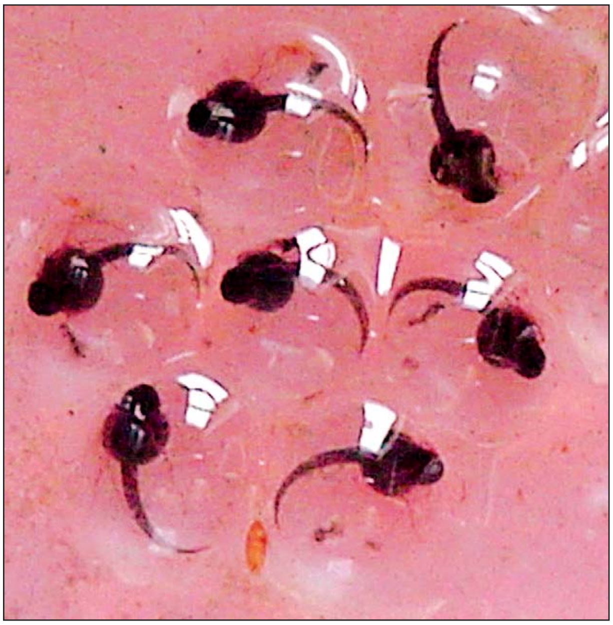
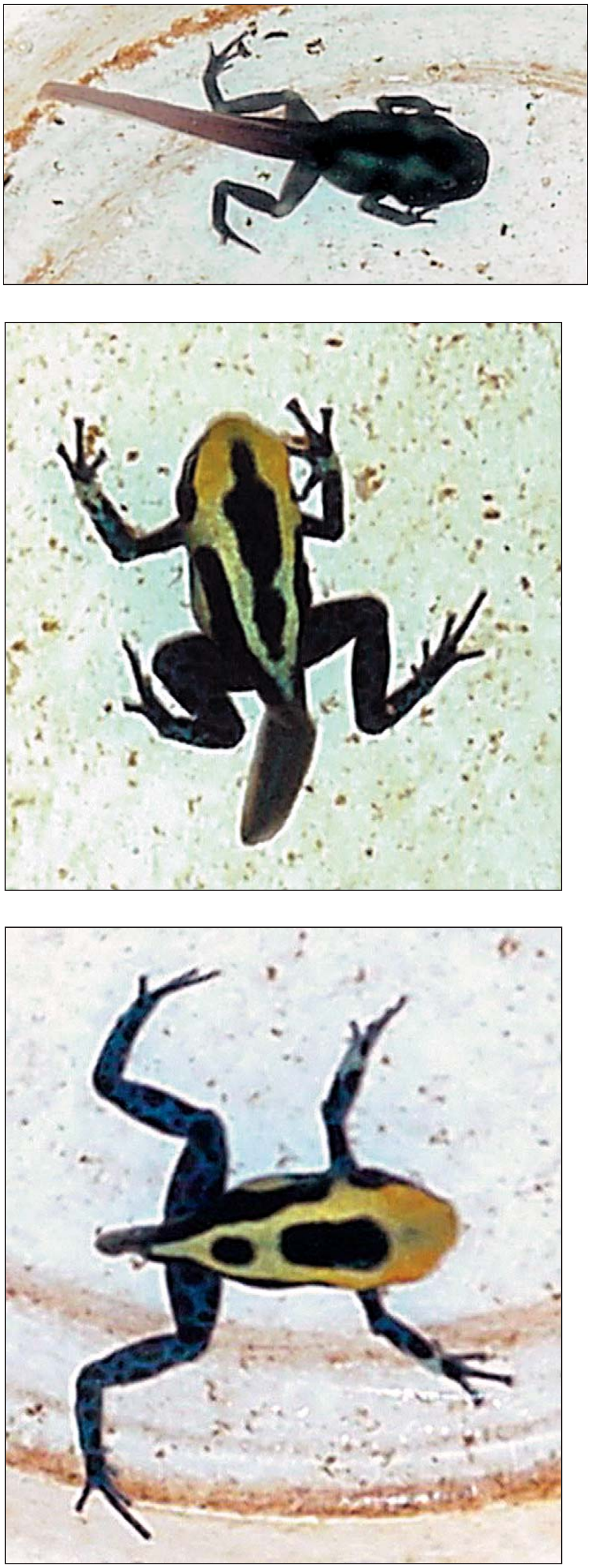


Figure 1.2 • Developing embryos of Dyeing poison frog *Dendrobates tinctorius*. (Photo by Helmer.)



Figures 1.3–1.5 • Progression of metamorphosis of Dyeing poison frog *Dendrobates tinctorius*. The process from egg to adult takes approximately 3 months. (Photo by Helmer.)

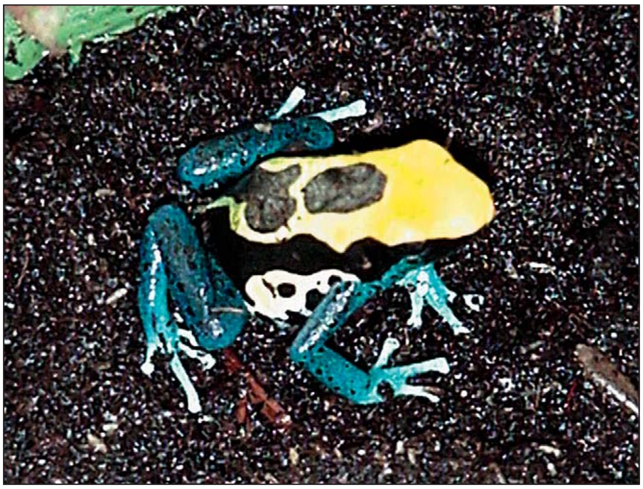


Figure 1.6 • Young adult Dyeing poison frog *Dendrobates tinctorius*. (Photo by Helmer.)

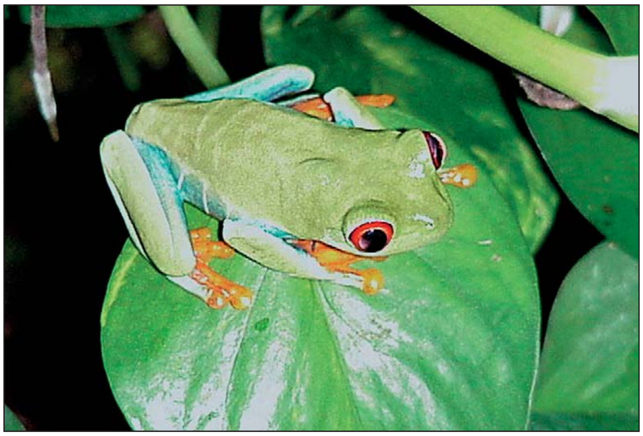


Figure 1.7 • Adult Red-eyed tree frog (*Agalychnis callidryas*). (Photo by Helmer.)

METABOLISM

Based on the theory of metabolic scaling, larger amphibians, in general, will require proportionately fewer calories than smaller animals. Metabolic requirements also vary with environmental temperature and activity level. Active, food-seeking species, such as Dendrobatid frogs, have a higher energy requirement than those species that ambush prey, such as the horned frogs (*Ceratophrys* spp.). Metabolic rate will increase by up to 1.5 to 2 times with illness or surgical recovery, and by up to 9 times with strenuous activity (Wright & Whitaker 2001). Formulae for the determination of metabolic requirements of various amphibians are presented in Table 1.5.

Thermoregulatory and hydrational homeostasis

Amphibians are poikilotherms (ectothermic), relying on a combination of environmental heat and adaptive behavior to maintain a preferred body temperature. This preferential temperature is dependent on a number of factors, including species, age, and season, and is essential for optimal metabolism. However, the ideal body temperature is also dictated by specific metabolic processes; for example, the body temperature required for optimal digestion is likely different from that required for gametogenesis (Goin et al. 1978; Whitaker et al. 1999; Wright 1996, 2001d).

A number of physiological and behavioral adaptations have developed in amphibians that allow them to control

Table 1.1 The class Amphibia is composed of three orders

Order	Representative species
Anura	Red-eyed treefrog (*Agalychnis callidryas*)
Gymnophionia	Caecilians
Caudata	Tiger salamander (*Ambystoma tigrinum*)

Table 1.2 Composition of the order Anura

Family	Representative species
Brachycephalidae	Saddleback toads
Bufonidae	True toads
Centrolenidae	Glass frogs
Dendrobatidae	Poison frogs
Discoglossidae	Painted frogs
Heleophrynidae	Ghost frogs
Hylidae	Treefrogs
Hyperoliidae	African reed frogs
Leiopelmatidae	Tailed frogs
Leptodactylidae	Tropical frogs
Microhylidae	Narrowmouth frogs
Myobatrachidae	Australian froglets
Pelobatidae	Spadefoot toads
Pelodytidae	Parsley frogs
Pipidae	Clawed frogs
Pseudidae	Harlequin frogs
Ranidae	True frogs
Rhacophoridae	Flying frogs
Rhinodermatidae	Darwin's frogs
Rhinophrynidae	Mexican burrowing toads
Sooglossidae	Seychelles frogs

Table 1.3 Composition of the order Caudata

Family	Representative species
Ambystomatidae	Mole salamanders
Amphiumidae	Amphiumas
Cryptobranchidae	Giant salamanders
Dicamptodontidae	American giant salamanders
Hynobiidae	Asian salamanders
Plethodontidae	Lungless salamanders
Proteidae	Neotenic salamanders
Salamandridae	True salamanders
Sirenidae	Sirens

Table 1.4 Composition of the order Gymnophiona

Family	Representative species
Caeciliidae	Common caecilians
Ichthyophiidae	Fish caecilians
Rhinatrematidae	Beaked caecilians
Scolecomorphidae	Tropical caecilians
Typhlonectidae	Aquatic caecilians
Uraeotyphlidae	Indian caecilians

Table 1.5 Formulae for determination of caloric needs of resting amphibians at 25° C

Order	Caloric requirement per 24 hours in kcal[a]
Anuran	$0.02\ (BM)^{0.84}$
Salamander	$0.01(BM)^{0.80}$
Caecilian	$0.01(BM)^{1.06}$

[a] Value should be increased by a minimum of 50% during periods of injury or illness.
BM represents the animal's body mass in grams.
(Adapted from Tables 7.1-7.4 in Wright KM and Whitaker BR, 2001).

their body temperatures to a limited degree. The most obvious of these are postural and locomotory controls that allow the amphibian to actively seek or move away from heat sources. Another important method of thermoregulation is peripheral vasodilation and constriction to regulate body core temperature, often in conjunction with glandular secretions to regulate evaporative cooling in some species (Goin et al. 1978; Whitaker et al. 1999; Wright 1996, 2001d). A change in skin color to modulate absorption of solar energy is another significant adaptation that has been studied in terrestrial anurans. Melanophores (melanin-rich pigment cells) in the skin of amphibians can regulate internal melanin aggregation or dispersal, thus changing the skin to a lighter coloration to enhance reflectivity, and thus decrease heat absorption in periods of light. In addition, some anurans have extraordinarily high skin reflectivity for near infra-red light (700–900 nm), owing to their iridophores (color pigment cells), which significantly reduces solar heat load (Kobelt & Linsenmair 1992, 1995; Schwalm et al. 1977).

Finally, a number of crucial physiological adaptations are found in wild temperate anuran and caudate species that are necessary for winter survival. These include protein adaptations (increased fibrinogen, shock proteins, and glucose transporter proteins, and the appearance of ice nucleating proteins in blood that guide ice formation), the accumulation of low molecular weight carbohydrates (glycerol or glucose) in blood and tissues, and increasing plasma osmolarity through dehydration. These adaptations serve to lower the freezing point of tissues (super-cooling) and promote ice growth in extracellular compartments. Amphibians that are freeze tolerant have also good tissue anoxia tolerance during freeze-induced ischemia (Lee & Costanzo 1998; Storey & Storey 1986).

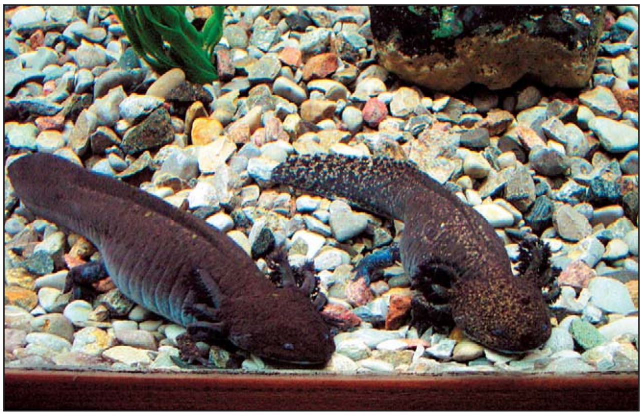


Figure 1.8 • Axolotl (*Ambystoma mexicanum*). (Photo by Whiteside.)

Physiology, behavior, pathology, and therapies are all influenced by temperature; therefore it is important for the clinician to realize that amphibians must be kept within environments that allow for them to stay within their preferred optimal temperature zone (POTZ) for normal metabolic homeostasis (Whitaker et al. 1999; Wright 2001d). It is equally important that amphibians not be subjected to rapid temperature fluctuations because thermal shock may ensue (Crawshaw 1998; Whitaker et al. 1999).

CLINICAL NOTE

Amphibians that are kept above their POTZ may show signs of inappetence, weight loss, agitation, changes in skin color, and immunosuppression. Those kept below the POTZ may become inappetent, lethargic, develop abdominal bloating associated with bacterial overgrowth from poor digestion, have poor growth rates, or become immunocompromised.

Thus enclosures that contain a mosaic of thermal zones are ideal to allow the amphibian to thermoregulate normally (Whitaker et al. 1999; Wright 2001d).

Due to the permeability of most amphibians' skin, desiccation is always a threat to survival, necessitating the development of physiological adaptations and behaviors to ensure hydrational homeostasis in aquatic or terrestrial environments. Amphibians are limited in their activities and ranges as their evaporative water loss is greater than that of other terrestrial vertebrates. Some species of amphibian, such as axolotls and mud puppies, are totally dependent on an aquatic environment, and even most terrestrial amphibians must remain moist in order for gas exchange to be effective (Boutilier et al. 1992; Shoemaker et al. 1992; Wright 2001d). For most captive amphibian species, a relative environmental humidity of greater than 70% is appropriate as it provides a humidity gradient and the animals can then select a level that is suitable for them. Clinicians should always remain aware of the need for the amphibian patient to remain in moist settings when being examined (Whitaker et al.1999).

Behavioral responses to minimize water losses include postural changes and limitation of activities to periods of elevated humidity. One well-documented physiological adaptation to prevent water loss that has been described in South American treefrogs (*Phyllomedusa* spp.), and likely exists in other treefrog species, is the secretion of a waterproofing substance from lipid glands in their skin (Heatwole & Barthalamus 1994; Wright 2001d). This waxy exudate is smeared over the surface of the frog with stereotyped movements of the feet and imparts a surface resistance to evaporative losses comparable to many reptiles. Other described physiological mechanisms in terrestrial amphibians include stacked iridophores in the dermis, and dried mucus on the epidermis (McClanahan et al. 1978; Wright 1996, 2001c). It is important to realize that these protective mechanisms are often lacking on the ventral surface of amphibians; the ventrum serves as an important route for water uptake from the environment, with some anurans even having a modified area on their ventral pelvis, known as a "drinking patch," that is responsible for up to 80% of water uptake (Parsons 1994).

CLINICAL NOTE

Absorption of water from the gastrointestinal tract is negligible in most species, thus oral fluids are of little benefit in rehydrating an amphibian. For most terrestrial species, shallow water soaks and subcutaneous or intracelomic dilute fluid administration are most effective in combating dehydration (Whitaker et al. 1999; Wright 2001d).

Aquatic amphibians face a different problem in that they are constantly immersed in a hypo-osmotic environment. Overhydration is a constant threat, with plasma expansion resulting in cardiac stress. To combat this, they have developed physiological mechanisms to excrete excess water while conserving plasma solutes (Goin et al. 1978; Mitchell et al. 1998; Wright 2001d).

GENERAL EXTERNAL ANATOMY

The three orders of amphibians are quite different in their external appearance. Salamanders are lizard-like in form, covered in glandular skin, have four legs (except the sirens, which are lacking the pelvic limbs), and lack claws on their digits. External feather-like gills may or may not be present. The tail is usually laterally flattened. The salamanders range in total length from 1.5 inches (4 cm) to over 60 inches (1.5m). The anurans, or frogs and toads, are tail-less as adults. External gills are absent. Anurans generally have longer hind legs than fore, and commonly have webbed, unclawed toes. Depending on the species, the glandular skin may be smooth or bosselated. The snout-to-vent length of anurans ranges from 3/8 inch to 12 inches (1–30 cm). Caecilians are limbless and resemble a snake or worm. They have a very short tail, if one is present at all. Small olfactory and sensory tentacles are present in the nasolabial groove just rostral to the eye. Total length varies from 3 to 30 inches (7.5–75 cm) (Stebbins & Cohen 1995; Wright 2001b).

SKELETAL SYSTEM

There is significant diversity of skeletal elements among amphibians. Caecilians lack pectoral and pelvic girdles, as well as the sacrum. Locomotion in this group is primarily achieved through worm-like regional contraction of the body (vermiform motion), or lateral, eel-like undulations (Stebbins & Cohen 1995; Wright 2001c).

Salamanders (Fig. 1.9) typically have four limbs, though the hindlimbs are greatly reduced in the mud eels (*Amphiuma* spp.) and missing in sirens (*Siren* spp. and *Pseudobranchus* spp.) (Stebbins & Cohen 1995; Wright 2001c). Generally, four toes are present on the forefoot and five on the hind, although this is variable between species. Salamanders are capable of regenerating lost toes and limbs. Cleavage planes, or predetermined zones of breakage, are present in the tails of many species so that when the animal is threatened or injured the tail breaks free of the body. This is known as *autotomy*; the lost tail will regenerate (Stebbins & Cohen 1995).

Anurans have several adaptations for saltatory locomotion or jumping. They have four limbs, and the hind legs are elongated (Fig. 1.10). There are generally four toes on the forefoot and five on the hind foot. The vertebrae are fused and the vertebral column is divided into the presacral, sacral, and postsacral regions. The sacrum itself is not present, and the pelvic girdle is fused. The forelimb is composed of the humerus, a fused radio-ulna, carpals, metacarpals, and phalanges, and the hind limb is formed by the femur, fused tibiofibula, tarsals, metatarsals, and phalanges. Caudal vertebrae are replaced by a fused

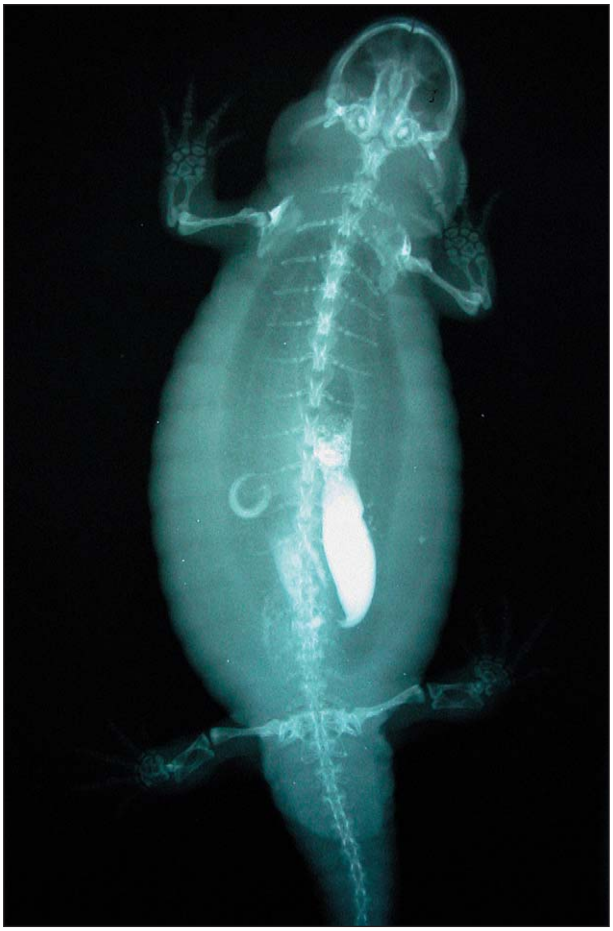


Figure 1.9 • Dorsoventral projection of gastrointestinal contrast study of a salamander. The radiograph is normal. (Photo by Whiteside.)

urostyle. Tadpoles can regenerate limbs, but adult anurans generally cannot (Wright 2001c).

CARDIOVASCULAR SYSTEM

The amphibian cardiovascular system is comprised of the arterial, venous, and well-developed lymphatic structures. The amphibian heart is 3-chambered, with two atria and one ventricle. The interatrial septum is fenestrated in caecilians and most salamanders, but complete in anurans, allowing varying degrees of mixture of oxygenated and deoxygenated blood (Wallace et al. 1991; Wright 2001c).

Blood draining from the caudal half of amphibians passes through the kidneys prior to entering the postcaval vein.

CLINICAL NOTE

Recent studies in reptiles have demonstrated little effect of the renal portal system on pharmacokinetics of drugs administered in the caudal half of the body (Holz et al. 1999, 2002); however, until similar studies are performed on amphibians it is advisable to avoid administration of medications in the hind limb or tail (if present) of amphibians.

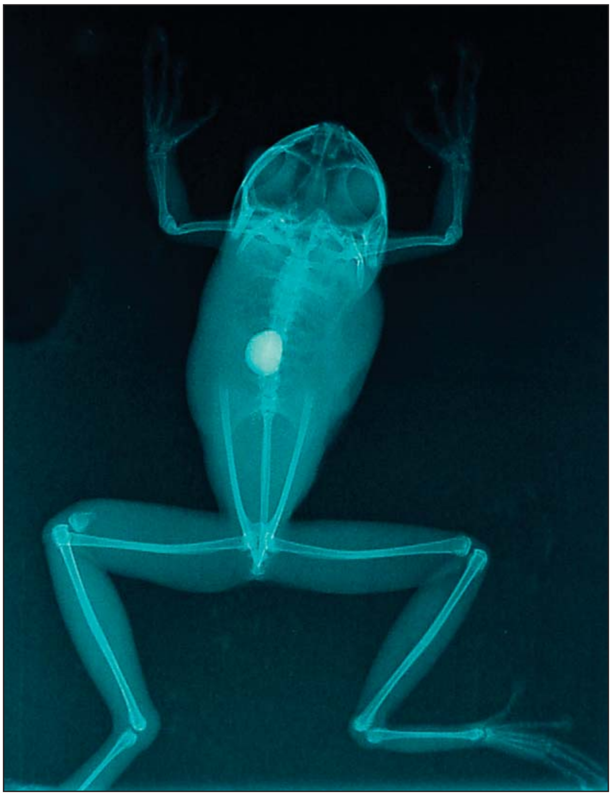


Figure 1.10 • Dorsoventral projection of a Red-eyed tree frog (*Agalychnis callidryas*). Note the fracture of the right femur, as well as the radio-opaque gastric foreign body. (Photo by Helmer.)

Amphibian lymph consists of all the components of blood, with the exception of erythrocytes. The lymphatic system includes lymph hearts (also known as lymph sacs or lymph vesicles) that beat independently of the heart at a rate of 50–60 beats per minute. These structures ensure unidirectional flow of lymph back to the heart (Wright 2001c).

Venepuncture sites

The choice of venepuncture sites will depend on the size and species of the patient. In anurans, potential sites include the:

- heart (cardiocentesis)
- ventral abdominal vein (often visible percutaneously in larger frogs) (Fig. 1.11)
- femoral vein
- lingual vein

In salamanders the ventral tail vein is readily accessible (Whitaker & Wright 2001).

IMMUNE SYSTEM

Hematolymphopoiesis

The cellular composition of the blood of amphibians consists of oval, nucleated erythrocytes, thrombocytes, monocytic cells (lymphocytes and monocytes), and poorly described

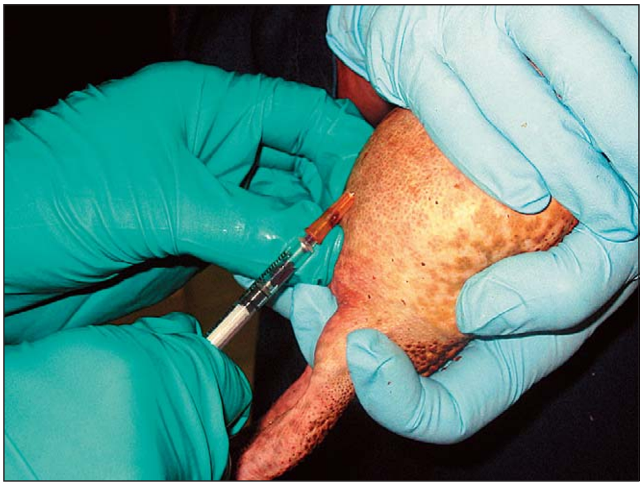


Figure 1.11 • Venepuncture of ventral midline abdominal vein of Marine toad (*Bufo marinum*). (Photo by Whiteside.)

granulocytic cells that are not homologous or analogous to mammalian granulocytes with similar staining characteristics (Wright 1996). Plyzycz et al. (1995) offer an excellent review of the hematolymphopoietic system of amphibians.

Bone marrow is found in a number of terrestrial amphibian species although it does not function to the same capacity as seen in higher vertebrates. Caecilians lack functional bone marrow, as do aquatic salamanders, relying on functionally equivalent centers in the liver and kidneys. Terrestrial salamanders have sites of lymphomyelocytopoiesis within their bone marrow, while the bone marrow of anurans serves only as a site for lymphocytopoiesis and myelothrombocytopoiesis (Goin et al. 1978; Wright 2001c).

The spleen of amphibians contains a mosaic of red and white pulp, which serve as centers of erythropoiesis and myelopoiesis respectively. All amphibians possess a thymus, which is one source of T-lymphocyte production, and remains functional throughout the life of the animal. The size of the spleen and the thymus can be affected by seasonal variations, and other factors such as malnutrition and chronic stress can lead to thymic involution. Amphibians lack lymph nodes; however, the intestinal tract contains scattered aggregates of lymphoid tissue known as gut-associated lymphoid tissue (GALT) (Plyzycz et al. 1995; Wright 2001c).

RESPIRATORY SYSTEM

In amphibians, gas exchange always occurs across a moist surface. Although cutaneous respiration is important in both larval and adult forms, as a general rule larval amphibians utilize gill structures for respiration, while adults use lungs, although there are many exceptions to this. There are three modes of respiration described in adult caecilians and anurans: pulmonic, buccopharyngeal and cutaneous. A fourth mode exists in adult urodeles, that being branchial respiration from retained gill structures seen in neotenic species such as sirens, mudpuppies, axolotls and Texas blind salamanders (Goin et al. 1978; Mitchell et al. 1988; Wright 1996, 2001c).

In most amphibians, gill structure shows some variability depending on the species and their environment. The gills of larval anurans are usually smaller and simpler than those of salamander larvae. While the branchial arches of tadpoles are covered by an operculum, in many species of salamander, especially neotenic species, the gills are external. The gills of most caecilians are resorbed before birth or hatching, while the gills of anurans resorb during metamorphosis. Most terrestrial salamander species lose their gills and develop lungs like anurans; however, many of the aquatic neotenic species will retain their gills and still develop normal lungs. A few families of salamander, notably the Plethodontidae and Hynobiidae, lack lungs or have lungs that are reduced in size (Goin et al. 1978; Mitchell et al. 1988; Wright 1996, 2001c).

The lungs of amphibians are simple saclike structures that lack true alveoli. As a result, most lungs are subdivided internally by delicate reticulate infoldings of the pulmonic tissue that significantly increase the surface area for gas exchange. Complete cartilaginous rings support the tracheal tissues. The trachea is variable in length depending on the species, but in general is considered short, and bifurcates quickly into main bronchi.

CLINICAL NOTE

Care must be taken if intubating the amphibian patient, or passing a tube to perform tracheal washes or intra-tracheal treatments, to prevent damaging the pulmonic epithelium. Also, owing to the delicate nature of the lung, one must make sure not to overinflate the lungs during anesthesia as they easily rupture (Green 2001; Mitchell et al. 1988; Wright 1996, 2001c).

Amphibians lack a diaphragm so they rely on coordinated movements of their axial and appendicular muscles for gas exchange in the lungs. Buccopharyngeal gas exchange occurs through the pumping action of the larynx during inspiration and expiration. During periods of reduced oxygen availability (such as hibernation) amphibians may switch to cutaneous respiration. As cutaneous respiration is not as efficient as pulmonic respiration, many amphibians have developed specialized integumentary structures, such as lateral folds, costal grooves or cutaneous "hairs", as seen in the African hairy frog (*Trichobatrachus* spp.) (Mitchell et al. 1988; Wright 1996, 2001c).

DIGESTIVE SYSTEM

Although many larval amphibians are herbivorous, adults are entirely carnivorous, with a wide variety of invertebrates constituting a large part of the diet. Caecilians rely primarily on olfactory cues to locate prey, whereas salamanders and anurans use sight as the prominent sense for food detection

(Stebbins & Cohen 1995). Prey movement triggers the feeding response. Anurans in particular are voracious feeders and tend to eat anything that fits in their mouth. Gastric overload and impaction, as well as ingestion of non-food items, such as substrate gravel or moss, are fairly common (Fig. 1.10).

Dentition

All orders of amphibians have "jointed" pediceled teeth. The crown is loosely attached to the base, or pedicel, of the tooth that is in turn attached to the jaw. Crowns are typically recurved in the direction of the pharynx and function in holding prey as opposed to chewing. The teeth are shed and replaced throughout life. Caecilians, salamanders, and some anurans have one or two rows of maxillary and mandibular teeth. Ranid frogs lack mandibular teeth, and bufid toads do not have any teeth. Many species also have vomerine and palatine tooth patches on the roof of the mouth (Stebbins & Cohen 1995; Wright 2001c).

Tongue

The tongue of most anurans and salamanders (caecilians have fixed tongues and pipid frogs are tongueless) can be extended beyond the mouth for food capture (Stebbins & Cohen 1995; Wright 2001c). In some species the tongue may be projected up to 80% of the total length of the animal (Mitchell et al. 1988). The tongue is extended and flipped (such that the posterodorsal aspect of the folded tongue becomes the anteroventral aspect), the surface of the tongue adheres to the prey item and is subsequently retracted into the mouth (Stebbins & Cohen 1995). The entire process may take as little as 50 milliseconds (Mitchell et al. 1988). Once in the mouth, the floor of the mouth is raised and the eyelids are closed, forcing the globes ventrally. This pushes the food item caudally into the pharynx.

Liver and intestinal tract

The remainder of the intestinal tract is relatively short and follows the normal vertebrate plan. Feces are expelled into the cloaca, a common opening for the gastrointestinal, urinary, and reproductive systems.

The amphibian liver is located posterior and ventral to the heart. The gross anatomy is variable depending on the taxonomic group but generally conforms to the body shape of the amphibian. Anurans have a bilobate liver, while caudates have a slightly elongated and marginated liver, and in the caecilians it is slightly marginated and very elongated. The gall bladder of all the groups is intimately associated with the liver, with a bile duct connecting it to the duodenum. In some species it joins the pancreatic duct before it enters the intestinal tract (Duellman & Trueb 1986).

From early embryonic stages through to the adult stage, the liver serves as an important erythropoietic center in amphibians. In addition, through the metamorphic stages, there is an increase in hepatic leukocyte production (Chen & Turpen 1995), and the liver plays an important role in immune function with its relatively large population of pigmented melanomacrophages and non-pigmented Kupffer cells (Gallone et al. 2002; Guida et al. 1998). The numbers of hepatic melanomacrophages in the amphibian liver are influenced by seasonal variation in some species, and increase with age and with antigenic stimulation in all species (Barni et al. 1999; Sichel et al. 2002; Zuasti et al. 1998). It is not uncommon to find melanomacrophages on celomic aspirates in amphibians with celomitis or ascites.

As with higher vertebrates, the amphibian liver also plays an important role in the synthesis of nitrogenous compounds, anti-oxidation reactions, metabolism of various endogenous and exogenous substances, glucose metabolism, protein synthesis, lipid metabolism, and iron metabolism (Crawshaw & Weinkle 2000).

URINARY SYSTEM

Amphibians have mesonephric kidneys that are unable to concentrate urine above the solute concentration of the plasma (Wright 2001c). A urinary bladder, which is bilobed in many caecilians, forms embryologically as an evagination of the cloaca. Urine passes from the kidney tubules into the collecting duct, into the cloaca, and then into the bladder. Thus urine is not expected to be sterile.

Amphibians excrete a variety of nitrogen wastes, based on habitat and the need to conserve water. Larvae and most aquatic adults excrete ammonia through the kidneys, skin, and gills, if present (Stebbins & Cohen 1995; Wright 2001c, 2001d). Terrestrial species convert toxic ammonia to less toxic urea in the liver. Urea can be stored in the bladder and excreted when water is readily available. Very specialized anurans, such as the waxy treefrog (*Phyllomedusa sauvagii*), are uricotelic, meaning they further conserve water by converting nitrogen wastes to uric acid. The clawed frog (*Xenopus laevis*) can convert from ammonia production to urea production based on the availability of water in the environment (Mitchell et al. 1988; Stebbins & Cohen 1995; Wright 2001c, 2001d).

REPRODUCTIVE SYSTEM

Amphibians have paired ovaries or testes. In the male, sperm travels from the testes, through the Wolffian duct, to the cloaca. In the female, follicles develop on the ovaries and, following rupture, the ova are released into the celom. Cilia in the celom direct the ova into the infundibulum and then into the oviduct (Stebbins & Cohen 1995; Wright 2001c). A notable anatomic feature of bufonid frogs is a Bidder's organ. This structure is a remnant of ovarian tissue found on the testes, and immature ova are evident histologically. This should not be interpreted as hermaphroditism (Green 2001; Stebbins & Cohen 1995; Wright 2001c).

Sexual dimorphism is present in some amphibians, but absent in many. Of the species commonly encountered in practice the following guidelines may be observed. In the bullfrog (*Rana catesbeiana*), males have larger tympanic membranes than females; male White's treefrogs (*Pelodryas caerulea*) develop nuptial pads during breeding season whereas females do not; the male dyeing poison frog (*Dendrobates tinctorius*) has large triangular toes, the female has smaller, more rounded toe tips, and the mature male red-eyed treefrog (*Agalychnis callidryas*) is smaller than the female (Stebbins & Cohen 1995; Wright 2001c).

Gonad activity and size fluctuate with reproductive state. Depending on the species, breeding season may be influenced by temperature, rainfall, or changes in day length. Vocalization of other individuals may also contribute to breeding synchrony among anurans (Stebbins & Cohen 1995).

Caecilians copulate and fertilize internally. The everted cloaca of the male forms the phallodeum, and deposits sperm into the female's cloaca (Stebbins & Cohen 1995; Wright 2001c). Approximately 75% of the caecilians are viviparous (Mitchell et al. 1988) and the oviductal lining may be consumed by the developing young as a food source (Wright 2001c).

A great majority of the salamanders are internal fertilizers. The males lack an intromittent organ, and instead deposit sperm packets, or spermatophores, on the substrate. The female picks up these packets through the cloacal opening and they are stored in the cloaca until egg laying. The exceptions are the Asiatic land salamanders (Hynobiidae) and the giant salamanders (Cryptobranchidae), which release sperm onto the egg mass once it is deposited outside the body (Stebbins & Cohen 1995; Wright 2001c).

The number and size of the ova produced vary greatly among species. The ova are typically surrounded by a translucent, gelatinous envelope and deposited in clusters in fresh water or moist terrestrial habitats. Melanic pigmentation of the ova is thought to protect against UV radiation and concentrate heat to warm them (Stebbins & Cohen 1995). Incubation duration varies from hours (24 hours for the black toad, *Atelopus* spp.) to several months. At the time of hatching, glands on the snouts of the larvae produce enzymes that dissolve the egg capsules. The duration of the larval stage depends on species and temperature (Stebbins & Cohen 1995; Wright 2001c).

ENDOCRINE SYSTEM

The endocrine system of amphibians has been well studied as a representative model for the vertebrate world, on account of the organs being very similar to those in reptiles, birds, and mammals. However, while the function of the various endocrine organs is similar to other vertebrates, the actual secretory products often have significant structural differences from their analogues in other vertebrates (Goin et al. 1978; Wright 2001c).

The adrenal glands of amphibians are found in close association with the kidneys, although their exact location varies tremendously with the species. Like reptiles and birds, the adrenal gland appears homogenous on cut surface, and histologically it is comprised of intermingled cortical and medullary elements, rather than having the clear delineation between cortex and medulla seen in mammalian species. The adrenal gland produces corticosteroids, adrenaline (epinephrine), and noradrenaline (norepinephrine) (Goin et al. 1978; Wright 2001c).

The thyroid is primarily responsible for controlling metamorphosis of larval amphibians, and like other vertebrates produces tri-iodothyronine (T3) and tetra-iodothyronine (T4). The thyroid gland is also responsible for the control of ecdysis. The hypothalamus is responsible for controlling pituitary gland secretion of thyroid stimulating hormone (TSH), which in turn controls production of T3 and T4. Neoteny is due to the failure of the hypothalamus to produce releasing factors that stimulate the pituitary gland to produce and release TSH. In facultative neotenic species, such as the Tiger salamander (*Ambystoma tigrinum*), deteriorating environmental conditions will trigger metamorphosis by stimulating the hypothalamus to start producing releasing hormone. However, in obligate neotenic species, which never undergo metamorphosis in nature, such as the Mexican axolotl (*Ambystoma mexicanum*), only the administration of thyroxine will result in completion of metamorphosis (Goin et al. 1978; Mitchell et al. 1988).

The pituitary gland is also responsible for the production of adrenocorticotropic hormone (ACTH), antidiuretic hormone (ADH), arginine vasotocin (similar to vasopressin in mammals), follicle-stimulating hormone (FSH), luteinizing hormone, (LH), melanophore-stimulating hormone (MSH), oxytocin and prolactin. The other endocrine organs (and their associated secretory products) are the gonads (estrogen, progesterone, testosterone), pancreas (insulin), parathyroid glands (calcitonin, parathyroid hormone), pineal body (melatonin), ultimobranchial bodies (calcitonin), and the thymus (thymosin) (Holz et al. 2002; Wright 2001c).

NERVOUS SYSTEM

The amphibian nervous system has been well studied for decades in a laboratory setting. As with all vertebrates a central and a peripheral nervous system exists. The brain is slightly more evolved than that of a fish, with only modest integrative capacity compared with the brain of avian or mammalian species. The medulla oblongata controls most of the bodily activities, while the cerebellum is responsible for controlling equilibrium, rather than fine motor coordination as seen in more developed tetrapod classes. The greatest brain development is for basic functions such as vision, hearing and olfaction (Goin et al. 1978; Mitchell et al. 1988).

There is considerable debate over whether there are 10 or 12 pairs of cranial nerves (CN), with those that are proponents of the lesser number classifying the spinal accessory nerve (CN XI) and the hypoglossal nerve (CN XII) as spinal nerves instead (Duellman & Trueb 1986; Goin et al. 1978; Mitchell et al. 1988). The spinal cord of caecilians and urodeles extends to the tip of the tail, while in anurans it ends in the lumbar region, with bundles of spinal nerves continuing through the spinal canal to form a cauda equina. As with higher vertebrates, there are enlargements of the spinal cord in the caudal cervical and lumbar regions, associated with limb movement, and development of brachial and inguinal plexi in amphibians with well-developed limbs (Goin et al. 1978; Wright 2001c).

The larval stages and aquatic adult forms of amphibians possess a lateral line system, which is absent in terrestrial amphibians. Lateral line nerves, derived from the cranial nerves, innervate this series of pressure-sensitive receptors on the head and along the sides of the body. The lateral line is responsible for perception of low-frequency vibrations and functions to detect stationary or moving objects by wave reflection (Goin et al. 1978; Mitchell et al. 1988; Wright 1996).

Senses

Hearing

Auditory structures vary greatly among amphibians, and in particular, the anurans have very well developed ear structures. An outer ear is lacking, and the tympanic membrane is responsible for transmission of high-frequency sounds to the bony columella in the middle ear, which then transfers it to the sensory patches in the membranous labyrinth of the inner ear. In many amphibian species, low-frequency sounds are transmitted to the inner ear by an opercular bone that receives the vibrations from the forelimbs (Goin et al. 1978; Mitchell et al. 1988; Wright 1996).

Sight

Ocular structures are well developed in amphibians, with the exception of caecilians and many cave-dwelling salamanders, and there has been further evolutionary development of tear glands and eyelids in terrestrial species. In order to accommodate, the lens is moved toward or away from the cornea, rather than changing the shape of the lens as in mammals. Pupillary diameter adapts to changes in environmental light; however, the iris is composed of striated muscle under voluntary control, which makes assessment of pupillary light responses problematic for the clinician. The retina of most terrestrial amphibians is complex, but vision in most amphibians is based on pattern recognition in the visual field rather than visual acuity. Several types of retinal ganglion cells respond to different features in the visual field, allowing the amphibian to construct a crude but useful picture of its surroundings. Approximately 90% of the visual information is processed in the retina, while only 10% is passed on to the optic lobes' reflex centers. This well-developed retina is thought to compensate for the relatively simple brain (Goin et al. 1978; Mitchell et al. 1988; Whitaker et al. 1999; Wright 1996).

Taste, touch, olfaction

These senses are well developed in amphibians. Taste buds occur on the tongue, roof of the mouth, and in the mucous membranes of the mandible and maxilla. Tactile receptors are scattered throughout the dermis. In addition to the specialized olfactory epithelium that lines the nasal cavity, amphibians also possess a sense organ known as Jacobson's organ. It consists of a pair of epithelial-lined blind-ended sacs connected by ducts to the nasal cavity and is innervated by a branch of the olfactory nerve. This organ is responsible for the detection of airborne chemicals, such as pheromones, and is thought to be important in regulating behavior rather than just food recognition (Goin et al. 1978; Wright 1996, 2001c).

INTEGUMENT

The integument of the amphibian is arguably one of the most important organ systems. The skin functions not only in a protective capacity but also as a sensory organ, and plays vital roles in thermoregulatory and hydrational homeostasis, sex recognition, and reproduction. Heatwole and Barthalamus (1994) provide an excellent review of the amphibian integument.

Like that of all vertebrates, the amphibian's skin consists of an epidermal layer and a dermal layer. Although the epidermis consists of several cell layers, it is considerably thinner than that of other tetrapods, with the stratum corneum usually consisting of only a single layer of keratinized cells in most species. In fact, some aquatic salamanders lack keratinization of the stratum corneum altogether. Shedding of the stratum corneum occurs regularly, and most amphibians will eat their skin sheds (Goin et al. 1978; Weldon et al. 1993). The basal epithelium is four to eight cell layers thick, and is the site of epidermal regeneration. Although the epidermis provides some protection from abrasive substrates, the epidermis is easily damaged if the amphibian is improperly handled or is in contact with inappropriate substrates. The resulting damages from even an apparently minor injury can have serious consequences as there is no longer an effective barrier against opportunistic microorganisms.

The well-vascularized dermis consists of an outer spongy layer (the stratum spongiosum), and a more compact inner layer (the stratum compactum). Capillaries, nerves and smooth muscle are found throughout the dermis. Some caecilians possess tiny dermal scales, not found in the other two orders. Three types of chromatophores that are responsible for skin coloration, as well as specialized glands, are present in the stratum spongiosum. In caecilians and salamanders, the stratum compactum contains collagen fibers that tightly adhere it to the underlying connective tissue, musculature, and bones, while in anurans there is not a tight association, resulting in a potential subcutaneous space for fluid administration. Due to this loose association, anurans (but not caecilians or salamanders) can appear edematous,

CLINICAL NOTE

When handling amphibians there is always some damage done to the epithelium; therefore, it is recommended that lightly moistened, powder-free latex or nitrile gloves be worn to minimize damage to the sensitive skin and decrease the transfer of microorganisms, or potentially noxious substances, from the hands of the clinician (Fig. 1.12).

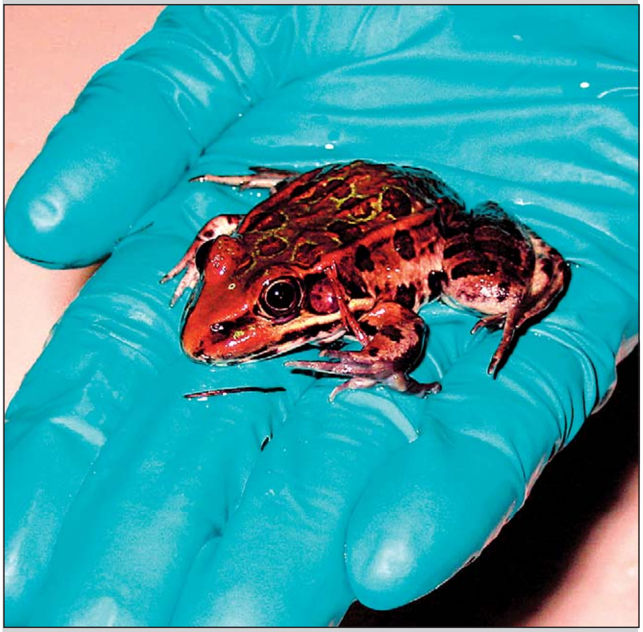


Figure 1.12 • Northern leopard frog (*Rana pipiens*) being appropriately handled with gloves. (Photo by Whiteside.)

CLINICAL NOTE

Amphibians are exquisitively sensitive to many toxic compounds at levels much lower than those that would cause clinical effects in higher vertebrates. It is also important to note that, owing to the thin nature of the epithelium, the skin represents an effective route for treatment in most amphibians, allowing topical administration of anesthetics such as MS-222 (tricaine methane sulfonate) or antibiotic, with resulting systemic effects (Whitaker et al. 1999; Whitaker & Wright 2001; Wright 1996, 2001c).

either as a result of normal water storage or due to pathological processes (Goin et al. 1978; Mitchell et al. 1988; Wright 1996, 2001c).

A variety of specialized glands are found within the epidermis and dermis. Some glands produce mucous or waxy substances to reduce evaporative water loss, as previously described. The dermis also contains numerous glands that produce toxic or irritating substances as protective mechanisms. Many of the glandular secretions of caecilians, salamanders, and anurans can be irritating to the mucous membranes of humans, while other amphibians, such as the arrow poison frogs (*Dendrobates* and *Phyllobates* spp.), produce steroidal alkaloid toxins that are potentially lethal to people. Some species, such as the fire salamander (*Salamandra salamandra*), can actually spray poison from dorsal glands, whereas others, such as the giant toad (*Bufo marinus*), have large parotid glands on the back of the neck that may spurt several feet when pressure is applied.

CLINICAL NOTE

The irritating, or even highly toxic, secretions from some amphibians are another reason why latex or nitrile gloves should be worn by the clinician, and in some cases eye protection also may be prudent (Goin et al. 1978; Mitchell et al. 1988; Whitaker et al. 1999; Wright 1996, 2001a, 2001c).

True scales and claws are lacking in amphibians, although some species have modified cornified epidermal claw-like structures, as seen in the African clawed frog (*Xenopus laevis*) and some salamanders, such as *Onchydactylus* spp. Other amphibians have different modifications, such as the cornified areas on the feet of Spadefoot toads (*Scaphiopus* spp. and *Pelobates* spp.) (Goin et al. 1978; Mitchell et al. 1988; Wright 1996, 2001c).

KEY POINTS

- The class name refers to the dual life stages: aquatic and terrestrial.
- Amphibians have a three-chambered heart (two atria and a ventricle).
- Aquatic larval forms use external gills for respiration and tend to be herbivorous, whereas terrestrial adults develop internal lungs and are carnivorous.
- All are poikilotherms (ectotherms).
- Gloves should be worn when handling amphibians to prevent damage to the patient and the handler.
- A specialized sensory organ in the oral cavity (Bidder's organ) is responsible for chemodetection.
- Most larval forms and some adult forms retain the ability to regenerate amputated tails, digits, and limbs.
- Phlebotomy sites include the heart, the ventral abdominal vein, the femoral vein, the lingual plexus, and the ventral tail vein (when present).

REFERENCES

Barni, S., Bertone, V., Croce, A. C., et al (1999) Increase in liver pigmentation during natural hibernation in some amphibians. *Journal of Anatomy 195*, 9–25.

Boutilier, R. G., Stiffler, D. F., & Toews, D. P. (1992) Exchange of respiratory gases, ions and water in amphibious and aquatic amphibians. In M. E. Feder & W. W. Burggren (eds.), *Environmental physiology of the amphibians*. Chicago: University of Chicago Press. pp. 81–124.

Chen, X., & Turpen., J. B. (1995) Intraembryonic origin of hepatic hematopoiesis in *Xenopus laevis*. *Journal of Immunology 154*, 2557–2567.

Crawshaw, G. J. (1998) Amphibian emergency and critical care. *The Veterinary Clinics of North America. Exotic Animal Practice 1*, 207–231.

Crawshaw, G., & Weinkle, K. (2000) Clinical and pathological aspects of the amphibian liver. *Seminars in Avian and Exotic Pet Medicine 9*(3), 165–173.

Duellman, W. E., & Trueb, L. (1986) Morphology: musculoskeletal, integumentary, sensory, and visceral systems. In W. E. Duellman & L. Trueb (eds.), *Biology of amphibians*. New York: McGraw-Hill. pp. 287–414.

Frank, N., & Ramus, E. A. (1995) C*omplete guide to the scientific and common names of reptiles and amphibians of the world*. Pottsville: Ramus Publishing.

Gallone, A., Guida, G., Maida, I., & Cicero, R. (2002) Spleen and liver pigmented macrophages of *Rana esculenta* L: A new melanogenic system? *Pigment Cell Research 15*(1), 32–40.

Goin, C. J., Goin, O. B., & Zug, G. R. (eds.) (1978) *Introduction to herpetology*, 3rd edn. San Francisco: WH Freeman. Structure of amphibians; pp. 15–38.

Green, D. E. (2001) Pathology of amphibia. In K. M. Wright & B. R. Whitaker (eds.), *Amphibian medicine and captive husbandry*. Malabar, Fla.: Krieger Publishing. pp. 401–485.

Guida, G., Maida, I., Gallone, A., Boffoli, D., & Cicero, R. (1998) Ultrastructural and functional study of liver pigment cells from *Rana esculenta* L. *In Vitro Cellular and Developmental Biology. Animal 34*(5), 393–400.

Heatwole, H., & Barthalmus, G. T. (1994) *Amphibian biology*. Vol.1, The Integument. Chipping Norton, UK: Surrey Beatty.

Holz, P., Barker, I. K., Burger, J. P., Crawshaw, G. C., & Conlon, P. D. (1999) The effect of the renal portal system on pharmacokinetic parameters in the red-eared slider (*Trachemys scripta elegans*). *Journal of Zoo and Wildlife Medicine 28*(4), 386–393.

Holz, P. H., Burger, J. P., & Pasloske, K. (2002) Effect of injection site on carbenicillin pharmacokinetics in the carpet python (*Morelia spilot*). *Journal of Herpetological and Medical Surgery 12*(4), 12–16.

Kobelt, F., & Linsenmair, K. E. (1992) Adaptations of the reed frog *Hyperolius viridiflavus* (Amphibia: Anura: Hyperoliidae) to its arid environment. VI: The iridophores in the skin as radiation reflectors. *Journal of Comparative Physiology [B] 162*(4), 314–326.

Kobelt, F., & Linsenmair, K. E. (1995) Adaptations of the reed frog Hyperolius viridiflavus (Amphibia, Anura, Hyperoliidae) to its arid environment. VII: The heat budget of *Hyperolius viridiflavus nitidulus* and the evolution of an optimized body shape. *Journal of Comparative Physiology [B] 165*(2), 110–124.

Lee, R. E. Jr., & Costanzo, J. P. (1998) Biological ice nucleation and ice distribution in cold-hardy ectothermic animals. *Annual Review of Physiology 60*, 55–72.

McClanahan, L. L., Stinner, J. N., & Shoemaker, V. H. (1978) Skin lipids, water loss, and energy metabolism in a South American treefrog (*Phyllomedusa sauvagii*). *Physiological Zoology 51*, 179–187.

Mitchell, L. G., Mutchmor, J. A., & Dolphin, W. D. (eds.) (1988) *Zoology*. Menlo Park, Calif.: Benjamin-Cummings. Amphibians; pp. 727–748.

Parsons, R. H. (1994) Effects of skin circulation on water exchange. In H. Heatwole, & G. T. Barthalmus (eds.), *Amphibian biology*. Vol 1, The Integument. Chipping Norton, UK: Surrey Beatty. pp. 132–146.

Plyzycz, B., Bigaj, J., & Midonski, A. (1995) Amphibian lymphoid organs and immunocompetent cells. In *Herpetopathologica*. Proceedings of the fifth international colloquium on the pathology of reptiles and amphibians. pp. 115–127.

Schwalm, P. A., Starrett, P. H., & McDiarmid, R. W. (1977) Infrared reflectance in leaf-sitting neotropical frogs. *Science 196*(4295), 1225–1227.

Shoemaker, V. H., Hillman, S. D., Hillyard, D. C., Jackson, D. C., McClanahan, L. L., Withers, P. C., & Wygoda, M. L. (1992) Exchange of water, ions, and respiratory gases in terrestrial amphibians. In M. E. Feder & W. W. Burggren (eds.), *Environmental physiology of the amphibians*. Chicago: University of Chicago Press. pp. 125–150.

Sichel, G., Scalia, M., & Corsaro, C. (2002) Amphibia Kupffer cells. *Microscopy Research and Technique 57*(6), 477–490.

Stebbins, R. C., & Cohen, N. W. (1995) *A natural history of amphibians*. Princeton, N.J.: Princeton University Press.

Storey, K. B., & Storey, J. M. (1986) Freeze tolerance and intolerance as strategies of winter survival in terrestrially hibernating amphibians. *Comparative Biochemistry and Physiology A 83*(4), 613–617.

Wallace, R. A., Sanders, G. P., & Ferl, R. J. (1991) The Chordates. In R. A. Wallace, G. P. Sanders, & R. J. Ferl (eds.), *Biology: The science of life*, 3rd edn. New York: HarperCollins. pp. 718–751.

Weldon, P. J., Demeter, B. J., & Rosscoe, R. (1993) A survey of shed skin-eating (dermatophagy) in amphibians and reptiles. *Journal of Herpetology 27*(2), 219–228.

Whitaker, B. R., & Wright, K. M. (2001) Clinical techniques. In K. M. Wright & B. R. Whitaker (eds.), *Amphibian medicine and captive husbandry*. Malabar, Fla.: Krieger Publishing. pp. 89–110.

Whitaker, B. R., Wright, K. M., & Barnett, S. L. (1999) Basic husbandry and clinical assessment of the amphibian patient. *The Veterinary Clinics of North America. Exotic Animal Practice 2*, 265–290.

Wright, K. M. (1996) Amphibian husbandry and medicine. In D. R. Mader (ed.), *Reptile medicine and surgery*. Philadelphia: WB Saunders. pp. 436–459.

Wright, K. M. (2001a) Evolution of the amphibian. In K. M. Wright & B. R. Whitaker (eds.), *Amphibian medicine and captive husbandry*. Malabar, Fla.: Krieger Publishing. p. 1.

Wright, K. M. (2001b) Taxonomy of amphibians kept in captivity. In K. M. Wright & B. R. Whitaker (eds.), *Amphibian medicine and captive husbandry*. Malabar, Fla.: Krieger Publishing. pp. 3–14.

Wright, K. M. (2001c) Anatomy for the clinician. In K. M. Wright & B. R. Whitaker (eds.), *Amphibian medicine and captive husbandry*. Malabar, Fla.: Krieger Publishing. pp. 15–30.

Wright, K. M. (2001d) Applied Physiology. In K. M. Wright & B. R. Whitaker (eds.), *Amphibian medicine and captive husbandry.* Malabar, Fla.: Krieger Publishing. pp. 31–34.

Wright, K. M., & Whitaker, B. R. (2001) Nutritional disorders. In K. M. Wright & B. R. Whitaker (eds.), *Amphibian medicine and captive husbandry*. Malabar, Fla.: Krieger Publishing. pp. 73–87.

Zuasti, A., Jimenez-Cervantes, C., Garcia-Borron, J. C., & Ferrer, C. (1998) The melanogenic system of *Xenopus laevis*. *Archives of Histology and Cytology 61*(4), 305–316.

2

General anatomy and physiology of reptiles

INTRODUCTION

Reptiles evolved from their amphibian ancestors about 250 million years ago (Evans 1986) and are now found on all continents except Antarctica. Some species like the Common adder (*Vipera berus*) and European lizard (*Lacerta vivipara*) can even be found as far north as the arctic circle. Chelonians (and the tuatara) are the oldest living reptiles and have been around for over 200 million years, while snakes are the most recent arrivals (Evans 1986). Unlike amphibians, which need to return to water to breed, reptiles can live independently of water and so can survive in a wider range of habitats, including arid desert conditions. They have achieved this by evolving scales to conserve water, laying amniotic eggs, and excreting insoluble uric acid.

Size

Reptiles have giant species like the Galapagos tortoise (*Geochelone nigra*) and anacondas (*Eunectes murinus*), but these are only found in the tropics. The majority of reptiles tend to be of smaller body size than mammals and birds, with most lizards weighing under 20 g (Pough et al. 1998a).

GENERAL INTEREST

The tuatara

The order Rhynchocephalia became virtually extinct over 65 million years ago and there are only two species of the tuatara (*Sphenodon punctatus*) remaining today (Fig. 2.1). The word tuatara means ‘peaked back’ in Maori, referring to its spiny crest. One species is found on islands off the coast of New Zealand while the other species is found only on North Brother Island in the Cook Strait. They are nocturnal, mainly insectivorous and, unlike other reptiles, which need temperatures of at least 19° C, can be active at temperatures as low as 11° C.

The tuatara is the most primitive of living reptiles. It resembles lizards in general body shape but unlike the other reptiles it has a fixed quadrate bone and lacks a copulatory organ. They have uncinate processes on the ribs, like birds, and gastralia or abdominal ribs, like crocodiles. They also have a much longer incubation period for the eggs, burying them for up to 15 months (Carroll 1979; Evans 1986; Pough 1998a).

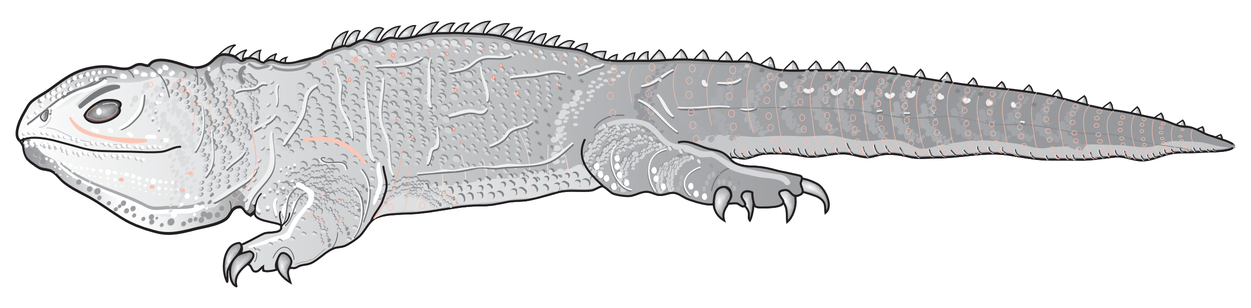


Figure 2.1 • The tuatara (*Sphenodon punctatus*) belongs to the order Rhynchocephalia and is the most primitive of living reptiles.

TAXONOMY

There are over 7780 species of reptiles in existence today (Uetz 2000), divided into four orders: Chelonia, Crocodylia, Rhynchocephalia and Squamata. This book will deal with the two orders more commonly seen in veterinary practice: the Chelonia, or shelled species, and the Squamata, which consists mainly of snakes and lizards (Table 2.1).

UNIQUE ANATOMICAL TRAITS OF REPTILES

- All reptiles have a protective layer of dry skin that has few glands and is keratinized to form either scales or scutes. A lipid layer beneath this keratin provides some resistance to water loss and this has helped them adapt to terrestrial existence (Lillywhite & Maderson 1982; Roberts & Lillywhite 1980).
- Reptiles only have a single occipital condyle articulating with the atlas. In contrast to amphibians they have a well-developed neck, which enables them to scan the horizon and survive on land (Bellairs 1969a).
- Many reptiles, like snakes and lizards, have a kinetic skull. This means that a large part of the reptile skull fails to ossify and elastic cartilage allows for movement between different regions of the skull. Consequently, reptiles are able to raise their upper jaw like a hinge to increase gape during feeding. The quadrate bone that articulates between the upper and lower jaw can also move freely.
- The transition to land has been facilitated by the development of an amniotic egg, enabling reptiles to breed independently of water. The production of a large yolked egg supplies a protective amnion and allantois for respiration and storage of waste products. The protective parchment-like shell prevents desiccation, allowing the embryo to become sufficiently developed before hatching (King & Custance 1982).
- Most reptiles excrete mainly insoluble uric acid instead of soluble ammonia and urea. This prevents waste products inside the impermeable egg becoming toxic to the developing embryo.
- With the exception of crocodiles, reptiles have a 3-chambered heart with two atria and one common ventricle. This allows reptiles to shunt blood either away or toward the lungs, facilitating thermoregulation and diving.

Table 2.1 Taxonomy and classification of reptiles (Uetz 2000)

Order	Suborder	Common term	No species (approx.)
Chelonia	Cryptodira	Turtles	295
	Pleurodira		
Squamata	Serpentes (Ophidia)	Snakes	2,920
	Sauria (Lacertilia)	Lizards	4470
	Amphisbaenia	Worm lizards	156
Rhynchocephalia		Tuatara	2
Crocodylia		Crocodile	23

METABOLISM

Reptiles have a much slower metabolism than mammals of similar size, with on average about one fifth to one seventh the metabolic rate at temperatures of 37° C (Bennett & Dawson 1976). The metabolic rate is influenced by many factors: it increases exponentially with rise in body temperature and smaller reptiles have a faster metabolism than larger ones. It can also vary between species: for example, the tuatara has one of the lowest metabolic rates whereas some Varanid (e.g., *Varanus gouldii)* and Teiid lizards (e.g., *Ameiva* spp.) have higher metabolic rates than most other lizards (Bennett, AF 1972; Espinoza & Tracy 1997).

Metabolism also depends on diet and predation behavior. Passive "sit and wait" reptiles, like pythons and boas, that wait to ambush their food as it passes by, have a much lower metabolism. In order to conserve energy their gastrointestinal tract shuts down in the months between each feed but they then experience a 7 to 17-fold (depending on species) increase in metabolic rate to help them digest their prey (Secor & Diamond 1995; Secor & Nagy 1994). Active predators, such as insectivorous lizards, that "seek and hunt" their prey, have higher metabolic rates and, as they feed daily, expend their energy maintaining their gut functions all the time (Secor & Diamond 1995; Secor & Nagy 1994).

Herbivorous species gain less energy from plant tissues and their digestive efficiency is 30–85% in contrast to 70–95% in carnivores. However, they spend a lot less time and energy acquiring their food than do the active foragers.

Anaerobic metabolism

Although aerobic metabolism utilizes energy more efficiently, the aerobic capacities of reptiles are much lower than endothermic mammal and birds. Reptiles switch to anaerobic metabolism for vigorous activities like diving, sprinting, chasing prey or escaping predation. This is independent of temperature but is a very high drain on energy reserves (up to 10 times).

During anaerobic exercise glycogen stored in the muscle is quickly broken down into lactate. As lactate is slow to be eliminated in reptiles they rapidly become fatigued and this is why reptiles can only sustain short bursts of intense activity. The increased lactate causes a drop in blood pH. This decreases the oxygen affinity of hemoglobin (Bohr effect) and consequently delays oxygen transport, further increasing the need for anaerobic metabolism (Bennett & Dawson 1976; Pough et al. 1998d).

THERMOREGULATION

Reptiles are ectothermic (Fig. 2.2), that is, they are unable to generate their own body heat and so rely on external sources to regulate their body temperature. This basically means that reptiles draw their heat from their environment and not from their food. Some metabolic heat is produced but the poor insulation due to the lack of fur and body fat means it cannot be retained. Thermogenesis is only reported in two species: the giant leatherback sea turtle (*Dermochelys coriacea*), which can retain heat because it has large amounts of body fat, and incubating female Indian pythons (*Python molorus*), which generate heat by muscle contractions (Bartholomew 1982; Bennett & Dawson 1976; Gregory 1982; Seymour 1982).

Advantages of ectothermy

The advantage of ectothermy is that reptiles do not waste energy maintaining their body temperature. While a small mammal, like a mouse, has high energy demands, a reptile of the same size will have just a tenth of the energy requirements. In fact, the food required by a small avian insectivore for 1 day would last a lizard of equivalent size about 35 days (Bennett & Nagy 1977). This lower food requirement and efficient food conversion has enabled reptiles to adapt to niche environments like arid deserts. It also enables them to survive hibernation and night cooling much better than mammals that need energy to keep warm at night (King 1996a; Pough et al.1998a).

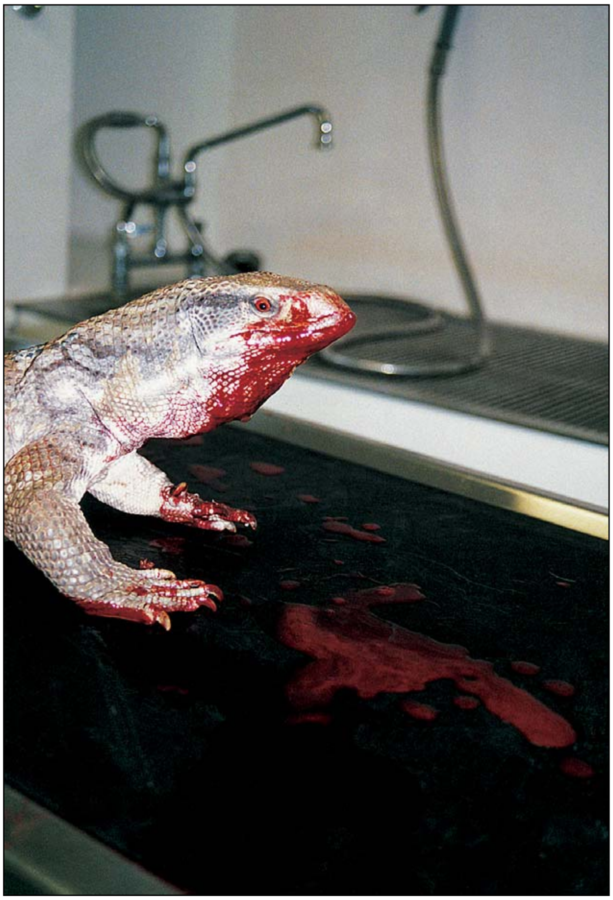


Figure 2.2 • As can be seen by this hemorrhaging Bosc monitor (*Varanus exanthematicus*), reptiles are not cold blooded as previously thought but are ectotherms.

Disadvantages of ectothermy

The main disadvantage of ectothermy is that all activity is limited by the ambient temperature. This means that the environmental range of reptiles can be limited and they become grounded when it is cold or at night. They are also unable to sustain high levels of activity for long because, unlike endotherms, they have poor aerobic capacity and so rapidly switch to anaerobic metabolism. This leads to fatigue when lactic acid builds up (King 1996a; Pough et al. 1998a).

Control of thermoregulation

Thermoregulation is controlled by the pre-optic nucleus of the hypothalamus in the brain. This receives blood from the heart via the internal carotid arteries. Temperature sensors can then stimulate behavior and physiological behavior according to the temperature. In lizards, the pineal gland and, in some species, the parietal eye may also play a role in regulating body temperature (Firth & Turner 1982; Pough et al. 1998c).

Preferred optimum temperature zone

The preferred optimum temperature zone (POTZ) is the temperature range of the reptile's natural habitat (Fig. 2.3). It can vary by 4–10° C, depending on the species, but is usually within a range of 20–38° C. The exception is the tuatara, which has a range of 12.8–20° C. Within this range, reptile species will have a preferred body temperature (PBT) for each metabolic function, like digestion and reproduction, which varies according to season, age, pregnancy, etc. (Pough et al. 2002b).

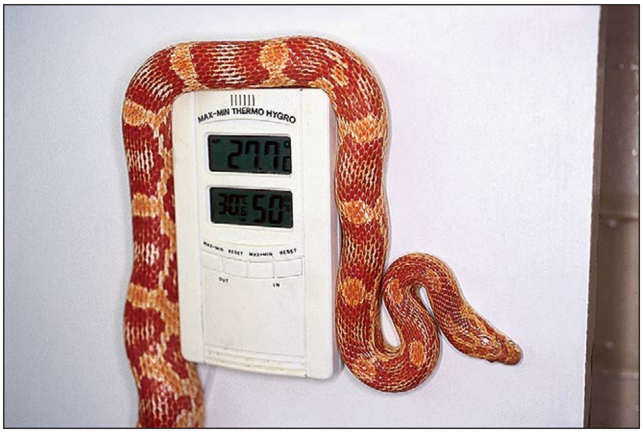


Figure 2.3 • All reptiles have a POTZ (preferred optimum temperature zone) which is the temperature range of their natural habitat. This cornsnake (*Elaphe guttata*) has a POTZ of 25–30° C.

CLINICAL NOTE

In order to be able to heat up and cool down a wild reptile follows a temperature gradient. For example, lizards will shuttle between basking in the sun to warm up and seeking shade to cool down. Consequently, in captivity both adequate temperature gradients and facilities to heat up and cool down must be provided (Barten 1996).

Behavioral fever

Sick mammals exposed to bacterial endotoxins release endogenous pyrogens which act on the hypothalamus to raise the temperature and create fever. This increase in temperature helps fight the immune system. Reptiles are unable to do this, but if ill or exposed to infection they actively seek extra heat; this is known as behavioral fever (Firth & Turner 1982).

Mechanisms of thermoregulation

Reptiles derive their heat via heliothermy or thigmothermy, or a combination of the two. *Heliothermy* means obtaining radiant heat by basking in the sun and is used by many diurnal reptiles, especially lizards. *Thigmothermy* is common in nocturnal or forest dwelling species, which acquire thermal energy via conduction with hot surfaces. The lack of insulation produced by scales enhances this thermal conduction (Bellairs 1969c; Espinoza & Tracy 1997).

Effect of heart rate and blood shunting

Reptiles have the ability to heat up faster than they cool down and this is facilitated by variations in heart rate and in blood shunting (Bartholomew 1982; White 1976).

- The reptile heart rate depends on many factors, such as temperature, body size and respiration rate. It increases as the body heats up and with active respiration but decreases during periods of apnea. In general, reptile heart rates are much lower than mammals but they can rise rapidly at high temperatures. This raised heart rate pumps warm core blood to heat up the periphery speedily. The reverse happens during night cooling (Bellairs 1969c; Firth & Turner 1982; Pough et al. 1998c).
- Their 3-chambered heart provides a rapid right to left cardiac shunt. This enables reptiles to bypass the evaporative process of the lungs completely and shunt blood systemically to avoid cooling.
- Vasomotor dilation and constriction of peripheral blood vessels also aids thermoregulation. During the day, the extremities heat up first and there is peripheral vasodilation. When temperature drops the heart rate slows down causing peripheral vasoconstriction, which results in blood being diverted rapidly to the core to prevent further heat loss (Pough et al. 1998c).

Body mass and shape

Many smaller reptiles have a high ratio of surface area to body weight and so lose and absorb heat rapidly. Large species have thermal inertia, that is, they take a long time to heat up and cool down, which enables them to resist rapid temperature change (Espinoza & Tracy 1997).

Reptiles can alter their body shape so that temperature can vary considerably along the body. In order to avoid exposing whole body parts to predators when it is cool, many lizards heat up their heads first in the morning and the body later. They can also lie flat on rocks for maximum heat exchange and elevate themselves onto their toes to reduce heat conduction and cool down in the hot desert sun. They also angle the long axis of their body perpendicular to the sun's rays to gain maximum heat, and face the sun when they want to cool down (Bellairs 1969c; Pough et al. 1998a; White 1976).

Behavior

Snakes and lizards tend to use much greater behavioral thermoregulation than chelonians, which have the shell to help retain heat. Snakes coil up to conserve heat and uncoil to cool down. Lizards select a dark background to heat up or even darken their skin by increasing melanin pigment at the skin surface (Espinoza & Tracy 1997). This darkened skin increases light absorption, which then converts into heat. Many lizards cool down by panting or gular fluttering, which is when they hold their mouth open and vibrate their throat, causing evaporation of water and cooling of the blood in this area (Bartholomew 1982).

Heat can also be lost by seeking shade, plunging into water or climbing higher in the trees to avail of the cooler convection currents. Some desert tortoises, which are unable to seek shade in rocks and crevices as easily as snakes and lizards, hypersalivate and even urinate for emergency cooling by evaporation (Bellairs 1969c; Minnich 1982).

Lighting

Ultraviolet light is important for behavior and vitamin D_3 metabolism. UVA (320–400 nm) affects behavior and well-being and helps trigger reproduction. UVB (290–320 nm) is necessary for the conversion of provitamin D_3 to previtamin D_3 (Fig. 2.4) and so is essential for calcium metabolism. Unlike mammals, reptiles utilize cholecalciferol (vitamin D_3) rather than ergocalciferol (vitamin D_2), so when supplementing reptiles only reptile vitamin supplements should be used. Where possible, the best source of UV light is unfiltered natural sunlight because artificial lighting cannot compare to the UV light from the sun (Boyer 1996).

HIBERNATION

Reptiles, having limited thermogenesis, rely totally on their environmental temperature. This means that reptiles inhabiting temperate climates and high altitudes have to hibernate when the temperature drops. However, some

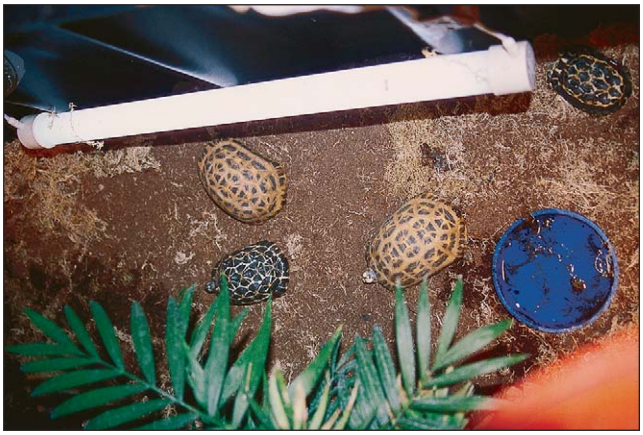


Figure 2.4 • Ultraviolet light is necessary for the conversion of provitamin D3 to previtamin D3 so is essential for calcium absorption.

species living at tropical high altitudes can absorb enough solar radiation by day to enable them to remain active and feed, even during the winter months (Gregory 1982).

Trigger factors to hibernation

In contrast to mammals, where hibernation is a survival mechanism triggered by scarce food supplies, hibernation in reptiles is governed mainly by temperature. The lack of internal thermogenesis, brown fat or shivering mechanisms makes this essential when the temperature drops. Captive reptiles, therefore, may not hibernate if kept in a warm environment. However, other factors like photoperiod, reproduction, food supply and body size also play a role, and endogenous rhythms may also play a part. In the wild, hibernation patterns can vary between the same species in different climatic ranges and even among different ages and sexes of same species (Gregory 1982).

Stages of Hibernation

1. Falling temperatures inhibit appetite.
2. The reptile seeks a hibernaculum. The main requirements are insulation against freezing (below the frostline) and some moisture to protect against desiccation. Oxygen tension is not important as many are tolerant of hypoxia.
3. Fat is stored in the liver, fat bodies of the celom, and tail and is the main energy source during and after hibernation. Metabolism slows down so that very little energy is actually used during the hibernation period. The main draw on lipid reserves is when the reptile emerges in spring.
4. Emergence from hibernation is triggered by rising temperatures and many will emerge early if the temperature improves. Photoperiod plays no role as most reptiles hibernate underground (Gregory 1982).

Hibernation and reproduction

The low temperature of hibernation helps synchronize the reproductive cycles together. Rising temperatures are also the cue for mating in spring and the males often emerge first. Reptiles that hibernate in a communal den often mate before dispersal. In some species appetite will not return until the mating process is over, so fat stores must last until then.

CLINICAL NOTE

A healthy tortoise emerging from hibernation should not have lost more than 10% of its body weight. This can be accounted for by (mainly) water loss but also some reduction in glycogen and lipids (Gregory 1982).

Aquatic hibernation

Water is very dense at the bottom of a pond and so does not freeze. Some freshwater turtles such as *Trionyx* spp. hibernate at the bottom of ponds during the winter months. They utilize anaerobic metabolism and breathe dissolved oxygen in the water through their skin (Seymour 1982).

Estivation

Inactivity during the dry season, *estivation*, is a strategy used by reptiles in hot deserts to conserve water. Trigger factors for estivation could be high temperatures or drought. Some turtles leave the water when it runs dry and bury themselves on land. During this process there will be progressive weight loss due to water and electrolyte loss.

KEY POINTS

- Reptiles, being ectotherms, are very dependent on their environment and this must be taken into account for those in captivity.
- Reptiles have 1/10 the food requirements of birds and mammals of equivalent size.
- The trigger for hibernation in reptiles is the fall in temperature.
- Not more than 10% body weight should be lost during hibernation.

SKELETAL SYSTEM

Bone structure

The mammalian haversian bone system allows for rapid remodeling of bone and the capacity for speedy transfer of calcium from plasma to bone. Such systems are lacking in lizards and snakes and are restricted to only certain cortical areas in crocodiles and chelonians (Enlow 1970). Therefore, remodeling is less a feature of bone healing in reptiles with less periosteal new bone. Bone healing is also much slower and it can take 6 to 30 months for full bone union.

Calcium / phosphorus

The bone contains about 99% of the body's calcium store (Boyer 1996). Plasma calcium must be maintained for vertebrate neuromuscular function so that, when ionized calcium drops, parathyroid hormone (PTH) increases and acts on bone to produce calcium and phosphorus. It also increases phosphorous excretion and stimulates further absorption of cholecalciferol from the small intestine. When plasma calcium levels are high calcitonin antagonizes PTH and stops calcium resorption from bone.

Nutritional osteodystrophies (metabolic bone disease) develop if the dietary input of calcium in captivity is not sufficient to replenish the bone reservoirs (Figs. 2.5 and 2.6). Reptiles have a Ca/P ratio of 2:1 but as they are commonly fed a diet rich in meat or insects, which have an inverse Ca/P ratio, metabolic bone disease is common. Herbivore diets are also low in calcium and phosphorus. Adult snakes that eat whole vertebrate prey rarely suffer from this problem, although it can be seen in juveniles (Boyer 1996).

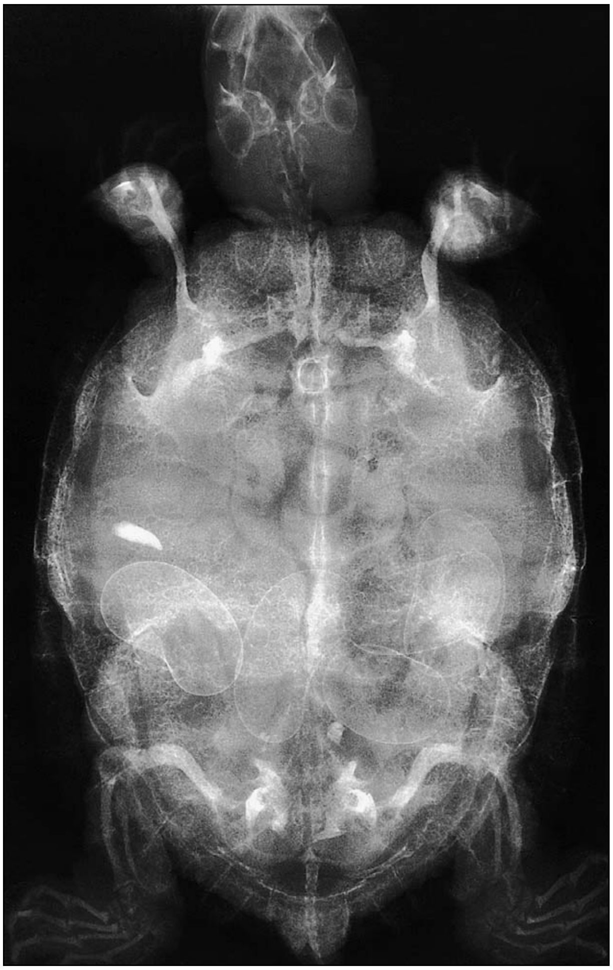


Figure 2.5 • Nutritional osteodystrophy (commonly called metabolic bone disease) in a Red-eared slider (*Trachemys scripta elegans*) fed a calcium deficient diet of prawns and chicken. The shell and limb girdles are severely demineralized with coarse bone trabeculae and there are thin-shelled and misshapen eggs (compare with shell in Fig. 3.14).

Reptile growth

In reptiles such as chelonians, snakes, and crocodiles the epiphyses never close so there is no skeletal maturity and some species keep growing all their lives. Lizards, however, do have secondary centers of ossification, like mammals, although these occur at a much later stage (Bellairs 1969a; Haines 1970). The rate of growth is much more variable than in mammals and will depend on food supplies, temperature and other environmental factors. Some reptiles, like pythons, can growth at a phenomenal rate in the early growth years.

Skull

The reptile orders have been classified into two subclasses based on the presence or absence of openings (fenestrae) in the temporal region of the skull (Fig. 2.7). These lie behind the eyes and provide better attachment points for the jaw musculature.

Chelonians belong to the subclass Anapsida (without arches) because they lack true temporal openings. However, many species do have gaps in the temporal region that provide a pseudotemporal fossa for muscle attachments. The tuatara, crocodiles and squamates all belong to the subclass Diapsida. Crocodiles and the tuatara have a true diapsid skull with a dorsal and lateral opening. Lizards have only one dorsal opening while snakes have an even more modified diapsid skull, having completely lost the upper temporal arch between the two openings (Bellairs 1969b; Carroll 1979; Pough 1998f). This has enabled the quadrate bone to move backwards and forwards in a condition called streptostyly.

Reptiles, like birds, have a cranial kinetic skull enabling the mouth to gape wide and this is highly developed in the snake where the jaw can literally walk along the prey being devoured. Lizards and crocodiles also have powerful snapping jaws. This is achieved by the adductor jaw muscles (Fig. 2.8) which arise from the temporal fossae and insert at right angles to the open jaw (King 1996b; King & Custance 1982).

Vertebrae

Reptiles do not need a rigid backbone to support the weight between their limbs as they normally have their belly on the ground; instead, flexibility of the spine is most important.

As reptiles have no diaphragm, and consequently no division between the thorax and abdomen, the terms thoracic and lumbar are redundant. Instead, the backbone can be divided into a presacral, sacral and caudal region. The number of presacral vertebrae varies from 24 in some lizards, 18 in Chelonia to 200–400 in snakes (Hoffstetter & Gasc 1970). The epaxial muscles lie dorsally while the hypaxial muscles are usually lodged ventrally and between the ribs.

The atlas and axis are more rigidly connected together than in mammals so the main center of movement is between the single occipital condyle and the backbone. Apart from

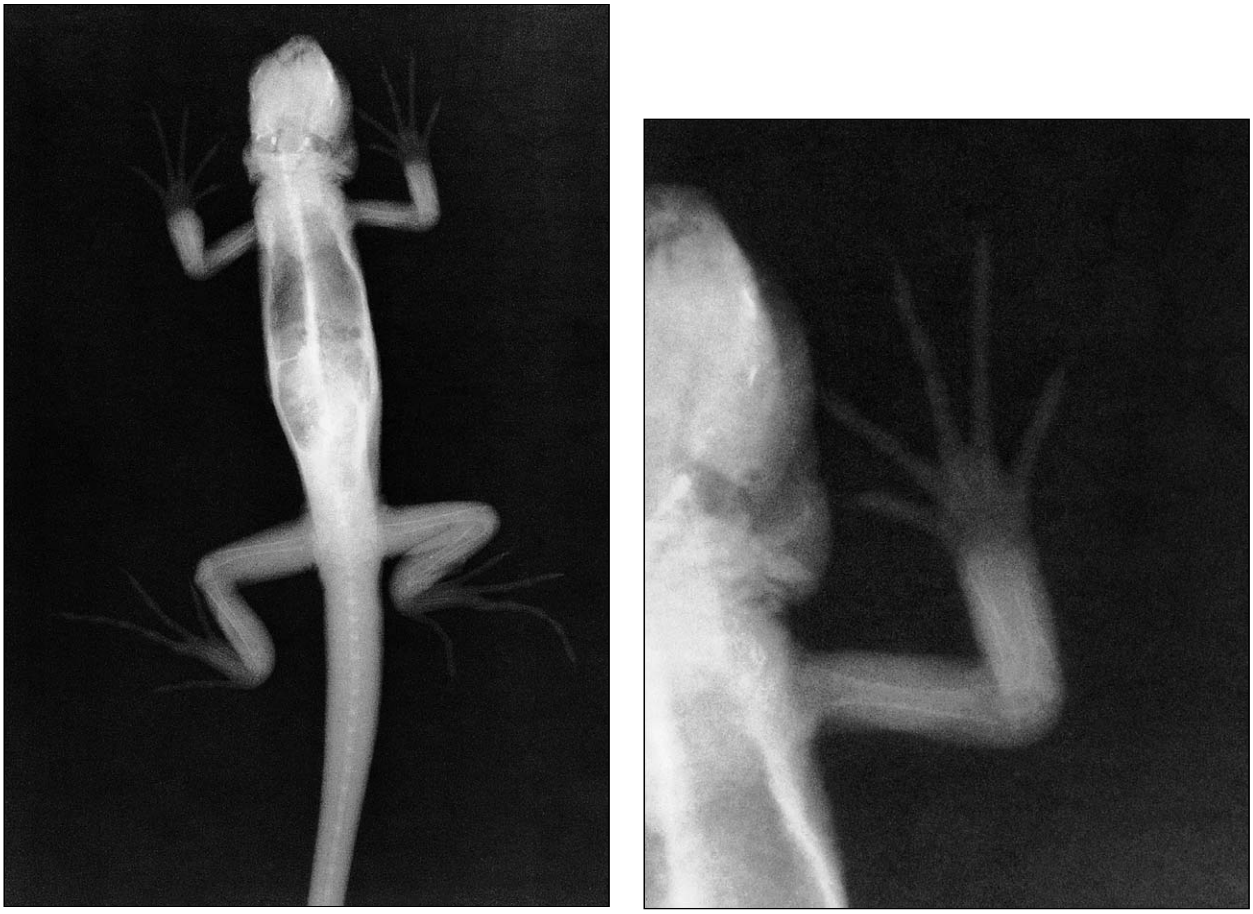


Figure 2.6 • Nutritional osteodystrophy in a juvenile Green iguana (*Iguana iguana*). The bone cortices are thin and shell-like with complete demineralization of such extremities as the feet and transverse processes of the tail (see close up of right foot and compare with normal skeleton in Fig. 4.12).

in Chelonia the ribs are well developed and, in addition to supporting the body wall, they perform the function of respiration and locomotion (Bellairs 1969a; Hofstetter & Gasc 1970).

CARDIOVASCULAR SYSTEM

The typical heart of snakes, lizards or chelonia has three chambers (two atria, one ventricle) whereas crocodiles have a 4-chambered heart. The right atrium receives deoxygenated blood from the systemic circulation via the sinus venosus. This is a large chamber that receives blood from the right and left cranial vena cava and left hepatic vein. There are also two aortae. The left aorta gives rise to a celiac, cranial mesenteric, and left gastric artery before uniting with the right aorta caudal to the heart. A renal portal system is also present (see Urinary system).

Although reptiles have only one ventricle it has three subchambers: the cavae venosum, arteriosum and pulmonale. Although there is no permanent division, the anatomical arrangement of the two atria, atrioventricular (a-v) valves, a muscular ridge, and the three subchambers creates a pressure differential. This, combined with the timing of ventricular contractions, means oxygenated and deoxygenated blood never actually mixes in the reptile heart (King & Custance 1982; Murray 1996a; White 1976).

The right atrium opens into the cavum venosum which gives rise at its ventral aspect to the paired aortas. The left atrium receives blood from the lungs via the left and right pulmonary vein and empties into the cavum arteriosum. The cavum pulmonale is the equivalent of the right ventricle in mammals and opens into the pulmonary artery. A muscular ridge partially separates this compartment from the cavum venosum and can redirect the blood flow (Pough et al. 2002a).

Normal intracardiac blood flow

Deoxygenated blood flows from the right atrium into the cavum venosum while oxygenated blood flows into the left atrium and cavum arteriosum. When the atria contract the a-v valves hinge medially to direct the flow of deoxygenated blood from the cavum venosum into the cavum pulmonale. When the ventricle contracts blood flows into the pulmonary

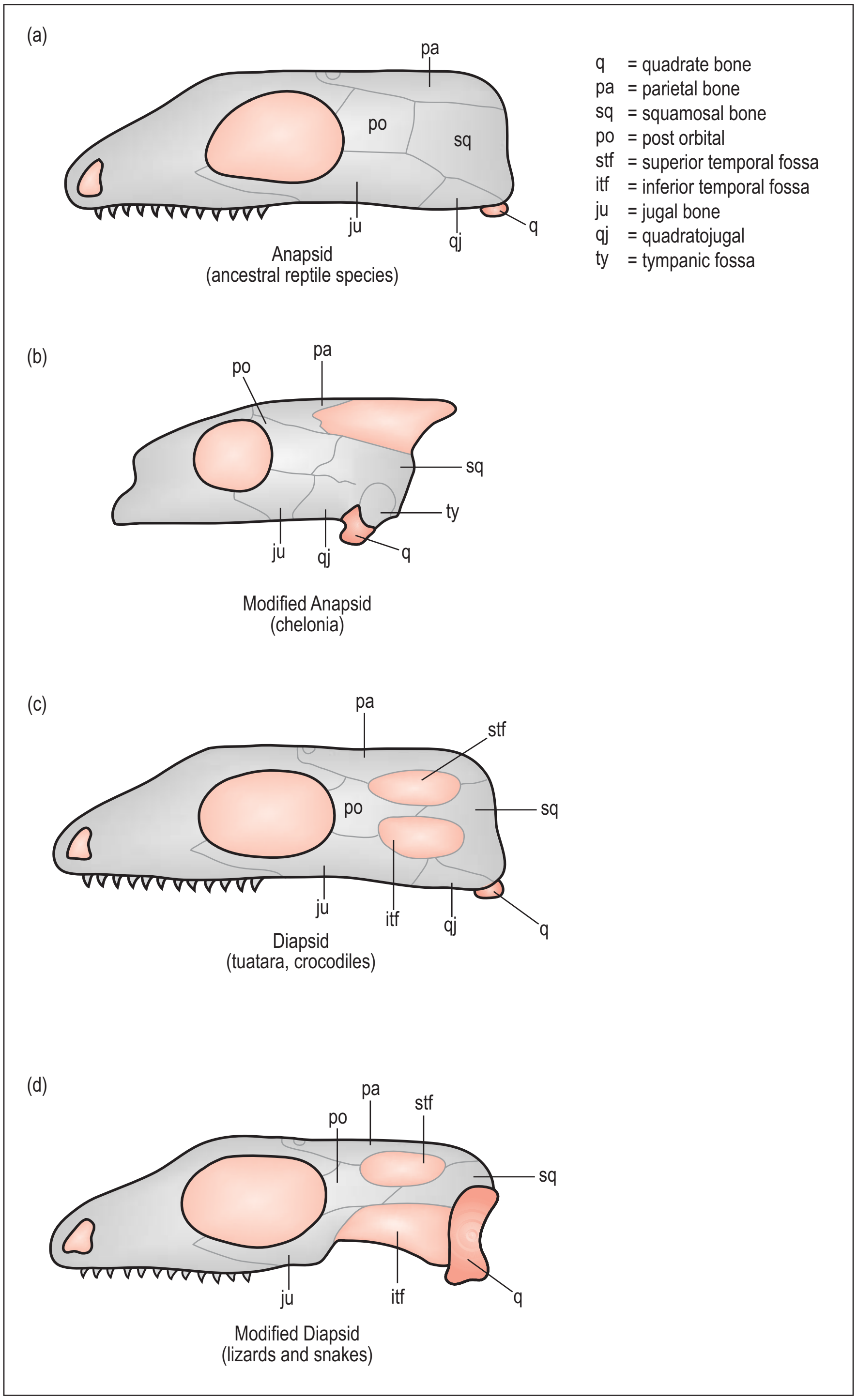

(a)
pa
po
sq
ju
qj
q
Anapsid
(ancestral reptile species)
q = quadrate bone
pa = parietal bone
sq = squamosal bone
po = post orbital
stf = superior temporal fossa
itf = inferior temporal fossa
ju = jugal bone
qj = quadratojugal
ty = tympanic fossa
(b)
po
pa
sq
ty
ju
qj
q
Modified Anapsid
(chelonia)
(c)
pa
stf
po
sq
ju
itf
qj
q
Diapsid
(tuatara, crocodiles)
(d)
pa
stf
po
sq
ju
itf
q
Modified Diapsid
(lizards and snakes)

Figure 2.7 • Diagram of skull.
(a) Anapsid (ancestral reptile species)
(b) Modified anapsid (chelonians)
(c) Diapsid (tuatara, crocodiles)
(d) Modified diapsid (lizards, snakes)

artery. The a-v valves close over allowing the oxygenated blood from the cavum arteriosum to flow into the cavum venosum and out into the aortic arches. The muscular ridge between the cavum pulmonale and cavum venosum prevents mixing of blood (Pough et al. 1998d, 2002a; White 1976).

Blood shunting

The circulation can be shunted depending on pulmonary resistance. During peak respiratory activity pulmonary resistance is low so deoxygenated blood flows through the pulmonary arch to the lungs while oxygenated blood travels systemically.

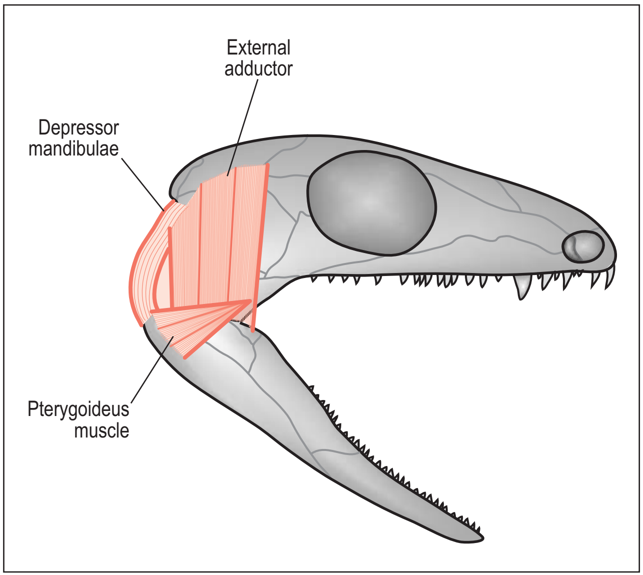


Figure 2. 8 • **Lateral view of reptile skull and jaw showing adductor muscles.**

In reptiles, which routinely experience periods of oxygen starvation (e.g., when turtles dive or snakes swallow large prey), the muscular ridge and a-v valves can divert blood away from the pulmonary circulation, where it is not needed, into the aortic arches and the systemic circulation. This right to left intracardiac shunt reduces blood flow to the lungs. This means less oxygen will be lost from the circulation and blood pressure will not drop as it passes through the capillaries of the lung.

Control of shunting

Shunting of blood is controlled by the differences in pressure between the pulmonary circuit and the systemic one. Normally the lungs provide little resistance to flow and the valves open first so blood flows through the lungs. However, during diving or apnea, vasoconstriction in the pulmonary arteries increases pulmonary resistance so blood is consequently shunted away from the lungs to the systemic circulation (Pough 1998d; White 1976).

ADVANTAGES OF INTRACARDIAC SHUNTING

- Ability to breath-hold while diving or inside shell
- Thermoregulation
- Stabilization of oxygen levels during intermittent breathing

CLINICAL NOTE

The ability of reptiles to divert blood away from the lungs via right to left shunts presents problems for anesthesia. It may also mean that chronic pneumonia or lung damage, which increase lung resistance, may also divert blood away from where it is most needed.

Heart rate

Heart rate varies with temperature, body size, respiration and stress. Larger sized reptiles have lower heart rates. It can also vary with activities like diving or breathholding (Murray 1996a). The Red-eared slider (*Trachemys scripta*) normally sends 60% of its blood flow to the lungs but while diving the majority of blood bypasses the lungs and enters the systemic network via the aortic arches. The heart rate slows down and total cardiac output falls. When the animal surfaces this is rapidly reversed in the first post-dive breath. (White 1976). This state can also occur even in terrestrial reptiles during apnea. Tortoises have been recorded to breathhold for 33 hours and even lizards like the iguana can breathhold for 30 minutes under water to escape predators (Pough et al. 1998d; White 1976).

Blood volume

The normal blood volume is approximately 5 to 8% of body weight. In a healthy reptile about 10% of this could be safely taken for blood sampling. The time of year, sex, and environment play a major role in hematological and biochemical blood parameters.

Blood cells

Reptile erythrocytes are nucleated and the lower metabolic rate of reptiles means they have a longer life span than mammals and birds (Bellairs 1969c; Campbell 1996). The hematocrit (average 20–35%) does not vary with high altitudes or hypoxia, as it does in mammals, but varies instead with temperature and season.

The white blood cells include heterophils (the equivalent of mammalian neutrophils), eosinophils, basophils, lymphocytes, and monocytes. Azurophils are unique to reptiles – they are similar to monocytes but have a red-purple cytoplasm and are a feature particularly of snakes (Campbell 1996; Redrobe & MacDonald 1999).

CLINICAL NOTE

Reptile erythrocytes are susceptible to lysis by EDTA anticoagulant. Lithium heparin is better for preventing clotting and preserving cell morphology, although fresh blood smears should always be made as well.

IMMUNE SYSTEM

The lymphatic system is more highly developed than the venous system in reptiles. Although they lack lymph nodes, reptiles have vast plexiform lymphatic networks and large dilated reservoirs (cisternae) that occur at the sites of mammalian lymph nodes. These are pumped by lymph hearts, which are smooth muscle dilations in the lymphatic channels located in the caudal part of the trunk. The main connection with the venous system occurs at the base of the neck where a saccular precardiac sinus passes lymph to the venous system (Ottaviani & Tazzi 1977).

The major lymphatic trunks are the jugular, subclavian, lumbar and thoracic. The jugular trunk drains the head and neck, the subclavian the forelimbs, the lumbar the hindlimbs, and the thoracic drains the trunk and celom. Both the lumbar and thoracic form a lymphatic dilation called the cisterna chyli.

The bone marrow, spleen, thymus and lymphatic system all play a part in immunoregulation. The paired thymus gland does not involute, although weight and size decrease with age (Bockman 1970). One or two yellow or white lobes are found on each side of the neck in lizards and chelonia and just cranial to the heart in snakes.

CLINICAL NOTE

Lymphdilution is a common contaminant of blood samples as the lymphatic system is so intimately associated with the blood. Dilution of blood samples will mainly affect the packed cell volume (PCV) and white cell count so a very low PCV should always be carefully evaluated.

KEY POINTS

- Snakes and lizards have a kinetic skull, which allows a wide gape.
- Metabolic bone disease is common in lizards and chelonia but not in adult snakes.
- The single ventricle allows blood to be shunted away from the lungs while diving or breathholding.
- Reptile erythrocytes are nucleated.
- Reptiles have a highly developed lymphatic system so lymphdilution of blood samples is common.

RESPIRATORY SYSTEM

Upper respiratory tract

In lizards the internal nostrils lie rostrally so that incoming air passes through the mouth on the way to the larynx. Snakes, however, have evolved a method of protruding the glottis and trachea out of the mouth while feeding. Chelonia and crocodiles (and some lizards) have developed a hard palate, which separates the air stream from the oral cavity.

The glottis in reptiles is situated quite rostrally, making them a relatively easy animal to intubate. The glottis remains closed at rest, opening only for respiration by the action of a glottis dilator muscle. Vocal cords are absent and sounds like hissing are produced by rapidly expelling air (Liem et al. 2001).

CLINICAL NOTE

Gular gulping or fluttering is not respiration but an olfactory process in chelonians and is used for courtship and territorial display in some lizard species. It is also used for evaporative cooling by vibrating the throat tissues to cool the blood passing through (Gans & Hughes 1967; McCutcheon 1943; Wood & Lenfant 1976).

Lower respiratory tract

Apart from gaseous exchange the lungs also play a role in display, buoyancy and vocalization (Perry & Duncker 1978). The lining of the respiratory tract has a primitive mucociliary apparatus, resulting in reptiles being poor at clearing inflammatory exudates from their lungs (Murray 1996c). In comparison to mammals, the lung volume of reptiles is quite large but they have only about 1% of the lung surface area of a mammal of equal size (Wood & Lenfant 1976). In aquatic species this larger lung volume may aid in buoyancy and act as an oxygen reservoir.

Reptiles have no diaphragm and so the combined pleuroperitoneal cavity is called the celom. More advanced species have a postpulmonary septum, which is a membrane that divides the pleural cavity from the peritoneal cavity. The lung parenchyma is simple and saclike and has a honeycomb network of faveoli, which are the reptilian unit of gaseous exchange (Perry 1989).

Reptile lungs are classified into three anatomical types according to the degree of partitioning of the lungs. The most primitive single-chambered (unicameral) lungs are found in snakes and some lizards. Paucicameral, found in iguanas and chameleons, have a few chambers but lack an intrapulmonary bronchus. The most advanced are the multichambered (multicameral) lungs found in monitor lizards, chelonia and crocodiles (Perry 1989; Perry & Duncker 1978). Many reptiles also have smooth muscles in the lung wall, which helps them inspire and expire air (Perry & Duncker 1978; Seymour 1982).

CLINICAL NOTE

The normal respiration rate is 10 to 20 breaths per minute, but this will vary with temperature and the reptile's size.

ACCESSORY RESPIRATORY SURFACES

(See Bellairs 1969c; Bennett & Dawson 1976; Seymour 1982; Wood & Lenfant 1986.)

In most species gas exchange is through the alveolar epithelium of the lungs but some reptiles can also breathe through accessory respiratory surfaces.

- Skin – some soft shell aquatic turtles (e.g., *Trionychidae*) can absorb oxygen through their skin and shell during submergence.
- Buccal–pharyngeal mucosa – used by many species of lizard.
- Tracheal lung – many snakes have a unique saccular diverticulum that acts in gas exchange.
- Cloacal bursae – in some freshwater turtles these have a highly vascular lining, allowing a high rate of oxygen intake from the water (Liem et al. 2001).

Ventilation

Despite their lack of a diaphragm reptiles draw air into their lungs by negative pressure breathing (Liem et al. 2001). A feature of all reptiles is a triphasic respiratory cycle of expiration, inspiration, and relaxation, which means oxygen concentrations in the lungs are constantly fluctuating. The relaxation or breathholding phase can be very long in aquatic species, lasting from 30 minutes up to 33 hours (Pough et al. 1998d; Wood & Lenfant 1976).

Reptiles can survive considerable periods at low oxygen levels as they are capable of converting to anaerobic metabolism while they breathhold. This tolerance to hypoxia seems to depend on the myocardium and ability to buffer lactic acid (Murray 1996c).

CLINICAL NOTE

Reptiles suffering from pneumonia and hypoxia will tend to seek lower temperatures to reduce the demand for oxygen.

Control of respiration

In mammals the acid base balance and PCO_2 are essential in controlling respiration. However, as reptiles are very tolerant of both anoxia and acid base change it is temperature that is the controlling factor. A rise in temperature increases the demand for oxygen, stimulating increased tidal volume. High oxygen tension decreases the respiration rate (Bennett & Dawson 1976; Murray 1996c; Wood & Lenfant 1976).

CLINICAL NOTE

As reptiles can survive long periods using anaerobic metabolism it is possible to revive patients with cardiopulmonary arrest by ventilating them at least once per minute with oxygen. Overventilation should not be performed because you run the risk of raising the PO_2 and depressing respiration further. Reptiles should be kept at their POTZ to trigger spontaneous respiration.

KEY POINTS

- Capacity for anaerobic metabolism
- Tolerance to acid-base imbalance
- Ability to breathhold for long periods
- Interventricular blood shunting
- Respiration rate varies with temperature and not PCO_2

DIGESTIVE SYSTEM

The reptile digestive tract is much shorter than that in birds and mammals and can vary from the simple tract of carnivorous species to the larger colons and cecum of herbivores. Carnivores use primarily fats and protein as food sources while herbivores utilize soluble carbohydrate and fermented fiber. Omnivores require a mix of fat, protein, and carbohydrate.

Dentition

Like mammals, reptile teeth are composed of enamel, dentine, and cement but lack a periodontal membrane. Three types of teeth exist, depending on feeding habits of the reptile: acrodont, pleurodont and thecodont (Table 2.2) (Fig. 2.9). *Acrodonts*, found in such lizards as water dragons and chameleons, have teeth attached to the crest of the bone. *Pleurodonts* have an eroded lingual side and are attached to a higher sided labial wall. (This is common in snakes and lizards like iguanas). *Thecodonts* are teeth embedded in a deep bony socket but, unlike in mammals, there is no periodontal membrane. This type is restricted only to crocodiles (Edmund 1970; King 1996a).

Reptile teeth are resorbed and replaced at a rapid rate throughout life. This is called *polyphyodonty* and is essential as their simple structure means frequent replacement is necessary to keep them sharp. In many cases the new tooth lies lingual to the old tooth and replacement occurs in a wave-like pattern from the back to the front. However, many acrodont reptiles cease producing new teeth after a

Table 2.2 Reptile dentition (Edmund 1970)

Type of dentition	Site of attachment	Examples
Acrodont	Crest of bone	Some lizards (water dragon, chameleons)
Pleurodont	Labial wall	Snakes, some lizards (iguanas)
Thecodont	Deep bony socket (no periodontal membrane)	Crocodiles

(See Fig. 2.9 for illustrations)

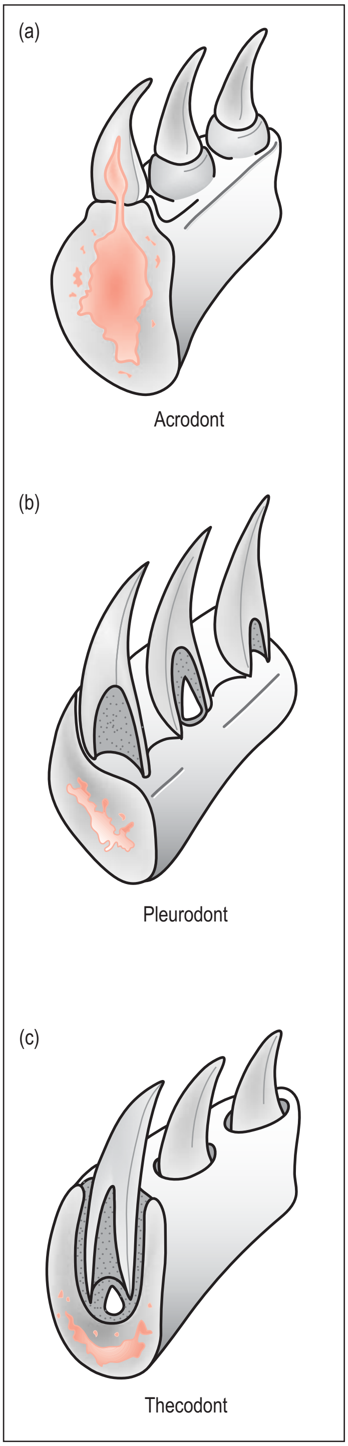


Figure 2.9 • Reptile dentition.
(a) Acrodont
(b) Pleurodont
(c) Thecodont

certain time, using the remaining teeth and jaw margins after these have been worn away (Edmund 1970).

Egg tooth

In snakes and lizards the egg tooth is modified from the normal teeth of the premaxilla and serves to rupture the embryonic membranes and shell in oviparous reptiles. In chelonians and crocodiles this is composed only of horny tissue and is called the egg caruncle.

Gastrointestinal tract

The absence of lips or flexible forelimbs, as in birds, means that reptiles rely on their jaw, and sometimes the tongue, to apprehend food. Mastication varies between species but is far less than in mammals. Reptiles have also evolved a complex system of oral secretory glands (e.g., palatine, sublingual, mandibular) to help them lubricate their prey. Many snake species have modified these glands into venom glands like Duvernoy's gland to help immobilize the prey and prevent damage to the delicate skull.

The stomach is small and contains hydrochloric acid, which prevents putrefaction, kills live prey, and aids digestion by decalcifying bone (Skoczylas 1978). Gastroliths are often seen on radiographs but, except in crocodiles, these may be accidentally ingested and play no role in normal digestion (Barten 1996). The liver is fairly large and in snakes it is very elongated. A gall bladder is usually present. Biliverdin is the main bile pigment; reptiles lack the enzyme biliverdin reductase which produces bilirubin. A cecum is prominent in herbivorous reptiles like the tortoise but is absent in most snakes. Reptiles do not have subcutaneous fat but store fat as "fat bodies" in the caudal celom or in the tail.

Cloaca

The rectum ends in a pouch called the cloaca (the Latin word for sewer). This consists of the anterior chamber called the copradeum, that collects the feces, a middle chamber called the urodeum where the ureters and reproductive system enter, and a posterior chamber called the proctodeum where all the wastes collect prior to excretion. These cloacal chambers are partially separated by transverse mucosal folds.

In desert species the cloaca plays an important part in water conservation. Food is often held in the lower gut for a minimum period for essential water absorption from excreta and urinary waste in the colon or cloaca. The final feces voided contains only the indigestible material like fur, hair, beaks, claws, eggshells, chitin remnants, and partially digested grasses (Bellairs 1969c).

Digestion of chitin

The exoskeleton of insects is composed of hard chitin, which is a polymer of acetylglucosamine and quite resistant to many chemicals. Insectivorous reptiles however have chitinolytic enzymes. Chitinase is secreted by the stomach and pancreas and occurs only in chitin eating species. This is the most important enzyme as it breaks open the exoskeleton and hydrolyzes it firstly into chitobiose and chitotriose (Skoczylas 1978). This in turn is acted on by the enzyme chitobiase, which breaks it into free acetylglucosamine. As this enzyme is not present in all insectivores it may play a lesser role in digestion. The rate of digestion will depend on the hardness of the exoskeleton (Skoczylas 1978).

Digestion of plants

Plants contain a lot of indigestible material like cellulose and lignin and are less susceptible to normal digestive juices. Hence, other methods like mechanical breakdown and symbiotic microorganisms have to be used. Herbivores use their teeth and jaw to mechanically grind their food and have microorganisms in their large intestine to ferment the food and break it down into volatile fatty acids. To facilitate this process they have a larger colon (in both length and volume) with a longer transit time than carnivorous species (King 1996c; Lichtenbelt 1992; Troyer 1984). Fiber is essential in the diet for gut motility. Herbivorous species also tend to be larger than equivalent carnivorous species and often show preference for young growing foliage, which has higher protein content and is more digestible. Digestive efficiency is, however, much lower than in carnivores (King 1996b).

CLINICAL NOTE

Gut transit time is slower in herbivores (King 1996c) and even slower in immunocompromised or sick animals. This is because the food is not masticated as well as in herbivorous mammals and the large colonic area slows the passage of ingesta down. The oral route of medication may therefore not be successful in very debilitated reptiles.

Feeding frequency

Unlike endotherms, which need to provide energy for body temperature maintenance, reptiles can survive on a fraction of the food input of birds and mammals (Bennett & Nagy 1977). Their low metabolic rate and high food conversion efficiency means they need much longer periods between feeds. Factors influencing feeding rates are temperature, size, reproductive status, health and season. Large carnivores such as pythons can last months between each feed. Reptiles undergoing ecdysis become anorexic before and during the shed.

Rate of digestion

The rate of digestion is related to temperature and low temperatures slow down gastrointestinal motility, secretion of digestive juices and metabolism (King 1996c). Digestion is sluggish between 10 and 15° C and stops at temperatures below 7° C. Transit time also depends on the composition of food, the length and activity of the gut, and the physical health of the animal. Herbivorous reptiles have longer gut transit times, often taking several days to digest food (King 1996c).

CLINICAL NOTE

At low temperatures, putrefaction and not digestion will take place. This is why hibernating species must be fasted before hibernating. As regurgitation is also the safety valve against putrefaction, this is why many reptiles (especially snakes) regurgitate at suboptimal temperatures. It is also important to make sure that tube-fed reptiles are kept at their PBT for digestion.

URINARY SYSTEM

The kidneys are located in the caudal celom. They are termed metanephric because they derive from the posterior embryo. Only chelonians and some lizards have a urinary bladder, and this is connected to the cloaca by a short urethra. Urine flows from the ureters into the cloaca and then into the bladder. Species with no bladder reflux the urine into the distal colon for water absorption (Davis et al. 1976). The bladder is often a reservoir of fluid in tortoises and, being osmotically permeable, substantial water can be reabsorbed from it in times of drought. Aquatic turtles use their bladder to help reabsorb sodium and as a buoyancy aid (Bentley 1976; Fox 1977; Minnich 1982).

Reptile kidneys lack a loop of Henle, pelvis, and pyramids. The reptile nephron consists of a glomerulus, a long, thick proximal convoluted tubule, a short, thin intermediate segment, and a shorter distal tubule. In male snakes and lizards the terminal segment of the kidney has become a sexual segment. This regresses after castration and is therefore under androgen control (Palmer et al. 1997).

Osmoregulation

Reptiles gain water mainly by consuming food and water; unlike amphibians, most reptiles do drink. Tortoises and snakes suck up fluids whereas lizards can lap with their tongues. There is also some minor absorption of water through the skin and by condensation in the nasal passages.

Water is lost from the body mainly by evaporation through the skin and mucous membranes but also by respiration, urine and feces. Cutaneous water loss will depend on the amount of skin keratinization and the size of scales. It is more common in desert species where there are high temperatures and low water saturation in the air. Shedding of skin (ecdysis) is also associated with an increased rate of water loss (Bentley 1976; Minnich 1982).

The reptile body mass is 70% water, which is similar to mammals but lower than amphibians' 75–80% (Bentley 1976). Total sodium and potassium are also similar to mammals but vary between species and habitat. The reptile kidney removes excess water, salts, and metabolic wastes. The lack of loops of Henle means that reptiles are unable to concentrate urine beyond the osmotic values of blood plasma. This could mean that excretion of solutes could draw copious amounts of water; however, the following methods are used by reptiles to conserve water.

METHODS OF WATER CONSERVATION IN REPTILES

- Uric acid
- Cloacal resorption
- Decrease in glomerular filtration rate
- Salt glands
- Renal portal system

Uric acid

Aquatic reptiles excrete ammonia and urea and relatively small amounts of uric acid, as water loss is not crucial. Terrestrial species need to conserve water so they excrete uric acid, which precipitates from solution in the bladder or cloaca to form pasty, white urates. These urates are either potassium or sodium salts depending on whether they are produced by herbivores or carnivores, respectively (Bentley 1976; Dantzler 1976; Minnich 1982).

The advantage of uric acid is that, being insoluble, it can be excreted with minimal water loss. The disadvantage, however, is that unlike humans, reptiles excrete uric acid through the kidney tubules, so dehydration does not stop uric acid excretion. If this builds up in the bloodstream of a reptile with dehydration or renal problems it easily causes gout. Gout results when insoluble uric acid accumulates and precipitates into urate crystals (tophi) that deposit in joints or visceral organs such as the pericardium, liver, and kidney. In can also occur when herbivorous animals like tortoises are fed animal proteins, leading to excess uric acid production and hyperuricemia (Mader 1996) (Fig. 2.10).

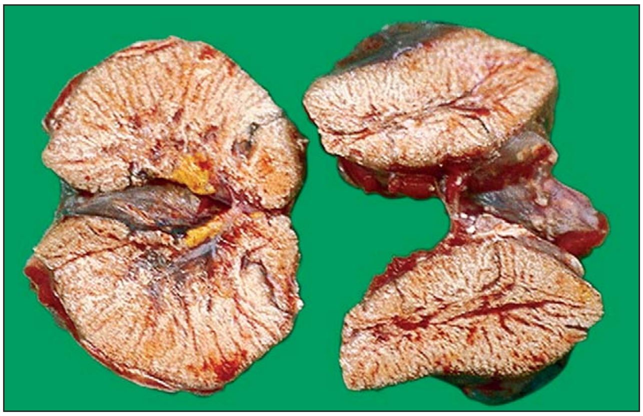


Figure 2.10 • Section of tortoise kidney showing renal gout. Reptiles being uricotelic easily develop gout when dehydrated. Hyperuricemia causes uric acid to precipitate into crystals or *tophi* in joints or visceral organs, like the kidneys.

CLINICAL NOTE

More than 60% of renal function must be lost in order to get a rise in plasma uric acid, so this is not a very sensitive parameter of renal function. Uric acid levels are also higher post prandially in carnivorous reptiles so fasting is important when testing the blood of such species.

Cloacal/colonic absorption

The cloaca, colon, and urinary bladder of reptiles play an important role in modifying urine produced by the kidneys. Active transport of ions and passive water absorption occurs through the colonic wall. The bladder also actively absorbs sodium but secretes potassium and urates (Bentley 1976; Minnich 1982).

CLINICAL NOTE

Collecting a voided or cloacal urine sample is not a true reflection of kidney function, owing to urine from the ureter being modified by cloacal reabsorption. Marine, desert, and most herbivorous reptiles also use salt glands, so even ureteral urine is not a true reflection of their osmoregulation.

Reduction in glomerular filtration rate

When a reptile is dehydrated or has a high salt load arginine vasotocin (reptile antidiuretic hormone) acts to constrict the afferent glomerular arterioles and decrease the glomerular filtration rate (Dantzler 1976). This causes decreased excretion of nitrogenous wastes and sodium, which in species lacking a salt gland leads to problems. Many desert species, however, have incredible abilities to tolerate severe dehydration together with a massive salt load. They can tolerate the elevated osmotic concentration and some lizards can even withstand a loss of water equivalent to 50% body weight (Bentley 1976). The Chuckwalla (*Sauromalus obesus*) from North Mexico survives without drinking, obtaining water from desert plants. It loses some water by evaporation and via cellulose in the feces and has salt glands to excrete potassium salts.

Salt glands

Reptiles do not have sweat glands or any method of losing salts through the skin. However, many reptiles have an extra renal salt gland to actively excrete potassium and sodium and conserve water. These vary in location but are usually found near the eye or nasal passages. With the exception of tortoises most herbivorous reptiles have salt glands from which they excrete more potassium than sodium. The Galapagos marine iguana (*Amblyrhynchus cristatus*) has one of the most active salt glands and this enables it to survive on a diet of marine algae (Bentley 1976; Dunson 1976; Minnich 1982).

CLINICAL NOTE

Reptiles with nasal salt glands sneeze excess salts when the plasma osmotic concentration is high. A clear fluid is produced that dries to form a fine white powder at the nostrils. This method of water conservation should not be confused with respiratory infection (Dunson 1976).

Renal portal system

The reptilian kidney has a dual afferent blood supply consisting of the renal arteries and the renal portal vein, which arises near the confluence of the epigastric and external iliac veins. This vein bypasses the renal glomerulus and enters the kidneys at the level of the kidney tubule where it plays a role in the secretion of urates. The renal portal system may play a role too in water conservation because, when the glomerular filtration rate slows down during dehydration, the renal portal system will keep perfusing the tubules to prevent necrosis (Holz 1999).

It is thought that, similarly to birds, reptiles have a valve system in place such that when the valve is closed blood flows through the kidney to the heart. However, under stress the valves open to bypass the kidney. The control of the valve is unknown but it may be opened by adrenaline and closed by acetylcholine, as in birds.

CLINICAL NOTE

As venous return from the hindlimb goes straight to the kidney tubules via the renal portal system, injecting drugs in the caudal half of the body could theoretically result in lower serum concentrations (Holz 1999). This could lead to underdosing and also renal toxicity from nephrotoxic drugs.

Nevertheless, this is unlikely to have much effect on therapeutics as it would only affect drugs excreted by tubular secretion; aminoglycosides like gentamycin and amikacin, which are excreted solely by glomerular filtration, would not be affected (Holz 1999). Although renal portal flow to the kidney increases when the animal is dehydrated, when the glomerulus is closed epithelial transport ceases. This means that although more drug may enter the kidney it will not necessarily be excreted (Holz 1999).

KEY POINTS

- Reptiles feed less frequently than mammals and birds.
- Herbivorous reptiles have longer gut transit times than carnivores.
- Digestion will not take place if the reptile is kept at suboptimal temperatures.
- Only Chelonia and some lizards have a urinary bladder.
- Dehydrated reptiles run the risk of developing gout.
- Reptile urine is not well concentrated and as it passes through the cloaca is not sterile.

REPRODUCTIVE SYSTEM

The pineal gland and the hypothalamus/pituitary gland interpret environmental stimuli into hormonal change to regulate reproduction. In temperate species, rising temperatures and increasing daylight stimulates the gonads wheras in tropical species food availability and rainfall are more important. If food is scarce the fat bodies will be used for nutrition rather than vitellogenesis and reproduction.

Hormones of reproduction

The main trigger of hormones involved in reproduction is increasing light. Melatonin, which is produced by the pineal gland, is only secreted at night so production declines when the days are longer, controlling the circadian rhythm. This stimulates the hypothalamus to produce gonadotropin releasing hormone (GnRH), which stimulates the anterior pituitary to produce luteinizing hormone (LH), and follicle-stimulating hormone (FSH).

In the female, FSH stimulates follicle growth while LH stimulates the production of sex steroid hormones, ovulation, and formation of the corpus luteum. Estrogen stimulates vitellogenesis of the follicles and LH surge, triggering ovulation. Post ovulation the regressing follicle becomes a corpus luteum and produces progesterone, which maintains the gravidity/pregnancy by inhibiting arginine vasotocin and prostaglandin in the uterine smooth muscle. When the corpus luteum regresses arginine vasotocin induces uterine smooth muscle contraction, which is then regulated by prostaglandins (Palmer et al. 1997).

Sexual maturity

This is related more to size than age and will vary with species. Small lizards reach maturity at 1–2 years but snakes can take 2–3 years. Chelonia can vary from 3 years in Red-eared sliders to 8 years in Box turtles (DeNardo 1996).

Sex determination

Two types of sexual determination can occur in reptiles:

1. Genotypic
2. Temperature-dependent sexual determination (TSD)

Genotype

Reptiles differ from mammals in that the female is heterogametic, being ZW, and the male is homogametic, being ZZ.

Temperature-dependent sex determination

TSD can occur in over 70 species of reptiles, including some lizards, the tuatara, turtles, and all crocodilians. So far research has found no evidence of TSD in snakes (Palmer et al. 1997).

In TSD, the sex of the embryo is not determined by sex chromosomes but by the incubation temperature during the early and middle incubation period. This is the period when the embryonic gonad develops into either testis or ovary. Although the full mechanism is still unknown it acts through the sex steroid hormones. It is thought that the different temperatures act on the aromatase enzyme complex that converts testosterone to estradiol. This then binds to estrogen receptors on the gonads to create females. To create males, enzymes convert testosterone to dihydrotestosterone, which binds to androgen receptors on the gonads and triggers males (Pough et al. 1998e). Although the range of temperature can be small the incidence of intersexes is in fact rare.

The advantage of this process is still uncertain but it may be a more primitive reptilian feature as it is found in the more ancient reptiles like tuatara, chelonia and crocodiles but appears not to occur in the more recently evolved snakes.

TEMPERATURE SEX DETERMINATION

Although the process is not clearcut, three patterns of temperature-dependent sex determination (TSD) appears to occur (Espinoza & Tracy 1997; Pough et al. 1998e; Thompson 1997).

- Crocodiles, some turtles and lizards (e.g., the Leopard gecko, *Eublepharis macularius*) produce females at both low and high temperatures but males at intermediate ones.
- Many chelonia produce females at high temperatures and males at low temperatures.
- Some lizards, such as the Rainbow lizard (*Agama agama*) produce the opposite: males at high temperatures and females at low temperatures.

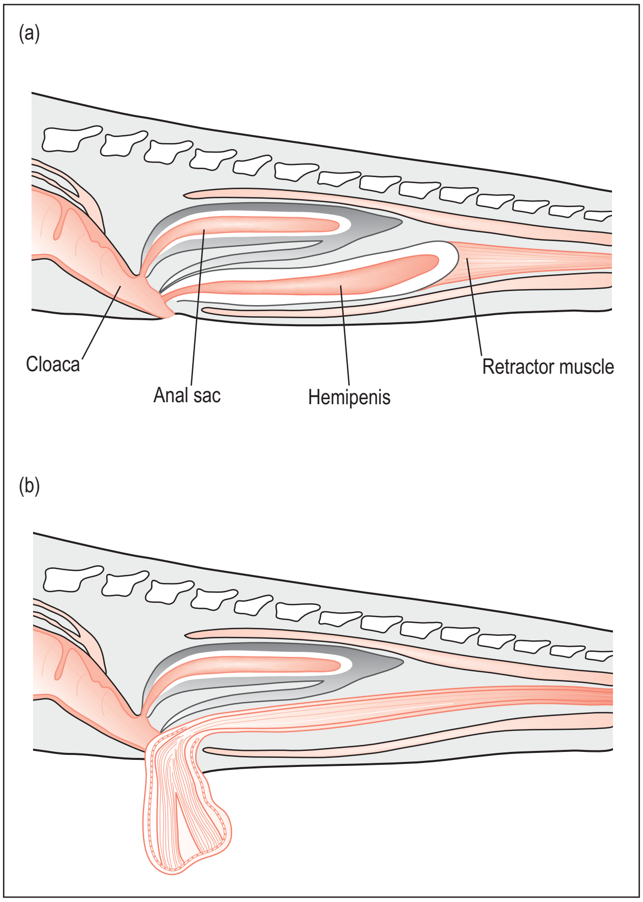


Figure 2.11 •
(a) Snake tail showing normal inverted hemipenis lying caudal to cloaca.
(b) Hemipenis everted out through cloaca.

The male

The testes produce the sperm and also secrete the hormones responsible for mating behavior and secondary sexual characteristics. Testicular size varies with season and therefore with light, temperature, and food supply. Male snakes and lizards have a renal sexual segment in the caudal half of the kidney. Secretions from this segment are transported to the cloaca where they are mixed with sperm (Bellairs 1969f; Palmer et al. 1997).

In both male and females the right gonad lies adjacent to the vena cava and is connected to it by very tiny vessels. The left gonad has it's own blood supply but lies intimately associated with the left adrenal gland.

Lizards and snakes have two extracloacal hemipenes. These lie side by side, just caudal to the cloaca, and are blind-ended organs containing walls of blood and lymph and a seminal groove. These become engorged and evert from their cavity for mating (Fig. 2.11).

Chelonia and crocodiles have developed the ventral proctodeum into a single unpaired intracloacal phallus. While this is protruded during copulation it is not turned inside out (Pough 1998b).

As can be seen in Figures 2.12 and 2.13, prolapse of the hemipenes or intracloacal phallus can be problems requiring surgery.

The female

The ovaries function in the production of estrogens and gametogenesis. They are saccular in shape and covered with a variety of follicles. There are two oviducts, which not only provide egg transport but also secrete albumin, protein, and calcium for eggshell formation. They can be divided into infundibulum, uterine tube, isthmus, uterus, and vagina that opens directly into the urodeum of the cloaca. In viviparous reptiles (see Viviparity) a large part of the uterus is thickened and muscular to hold the developing embryo (Palmer et al. 1997).

The ovarian cycle of mature reptiles is divided into three phases (Palmer et al. 1997).

1. Quiescent – This is where there is no development of the ovary or oviduct.

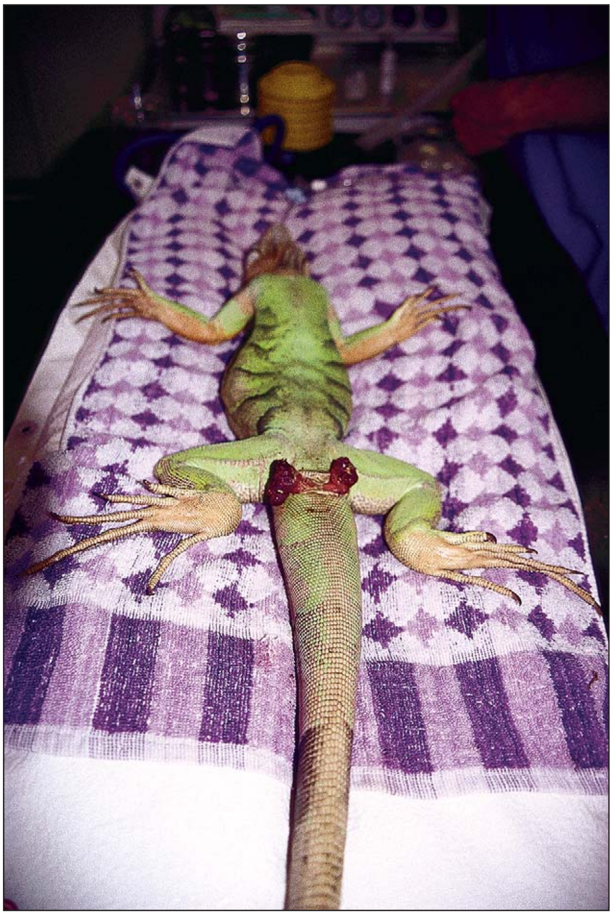


Figure 2.12 • This Green iguana (*Iguana iguana*) had a prolapse of both hemipenes of 3 days duration. They were necrotic so it was too late to replace them and they were surgically amputated.

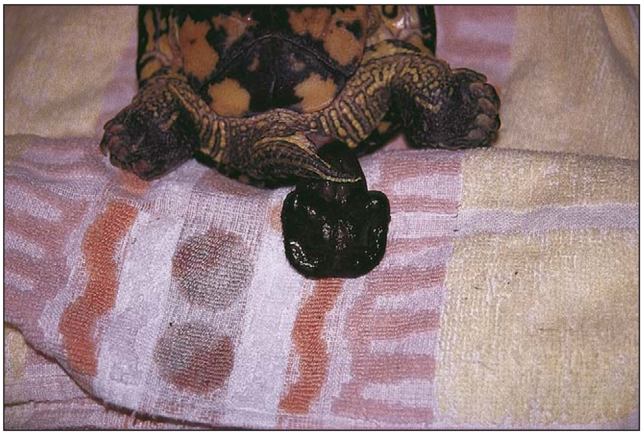


Figure 2.13 • Prolapsed phallus in a Red-eared slider (*Trachemys scripta*) secondary to debilitation.

2. Vitelligenic – This is the phase of rapid hypertrophy of the ovaries and oviduct. Under the influence of estrogen, yolk is produced by the liver and transported via the blood to the maturing ovary. The largest follicles mature first and become heavily filled with yolk. Increased estrogen activity mobilizes calcium from the bone into the bloodstream and can cause serum levels to rise two- to four-fold (Campbell 1996). The increase in serum calcium is concomitant with serum lipid being drawn from the fat bodies.
3. Gravidity/pregnancy – The gestation period is from the time of fertilization to oviposition, not from the time of mating. The terms *gravidity* and *pregnancy* refer to the presence of either eggs or embryos within oviduct following ovulation. The follicle then becomes the corpus luteum, which secretes progesterone to maintain the gravid or pregnant state and inhibit oviposition or parturition. Most species have a pre-lay shed (ecdysis) before oviposition and this is usually the signal to provide the reptile with a nest (DeNardo 1996).

Sperm storage

Fertilization is always internal in reptiles. Many species of snake and turtle can store sperm so that mating can occur in one season and reproduction in the next. In these species, sperm is stored in the oviduct and fertilization is triggered when the ova enter the oviduct months later. Sperm storage can range from several months to 6 years (Bellairs 1969f; Fox 1977; Seymour 1982).

Reptiles can be oviparous or viviparous (Palmer et al. 1997). The term ovoviviparous used to be used for an intermediate stage where the embryo was ready to hatch, just as the egg was laid. It was previously thought that there was no placental transfer of nutrients in these cases but when ovoviviparous species were studied in more detail it was found that some form of exchange usually exists, render-ing the term redundant. For example, the garter snake (*Thamnophis sirtalis*) has placental exchange yet lays an soft membrane egg.

Chelonia and crocodiles always lay eggs, so it is only lizards and snakes that have evolved viviparity. The eggs of crocodiles, some turtles, and geckos are hard shelled while most snakes and lizards have softer more parchment-like shells (Palmer et al. 1997; Pough et al. 1998b; Thompson 1997).

Oviparity

In oviparous reptiles eggs are laid quite early and the embryos are relatively undeveloped. The eggs are white with soft, but tough, leathery shells and contain a large amount of yolk. This yolk is the only source of nutrients to the developing embryos and is rich in fat, protein, and calcium. Oviparous species can produce 2–3 clutches during the breeding season but are unable to reproduce in cold climates because low temperatures would prevent the eggs developing. Examples include most colubrids, iguanas, monitors, geckos, and all chelonia and pythons (Bellairs 1969f; DeNardo 1996; Palmer et al. 1997).

Viviparity

Viviparity involves some form of placental exchange between mother and fetus and may have evolved to help offspring survive in cooler climates (Bellairs 1969f; Palmer et al. 1997; Pough et al. 1998e). The corpus luteum is maintained and secretes progesterone, which inhibits oviduct contraction. The main disadvantage of viviparity is that the female is more vulnerable to predation during gestation and can only have one clutch a year as gestation can last from 1.5 to 6 months. The added space of the fetuses also puts pressure on the gastrointestinal tract so pregnant females dramatically lose condition (DeNardo 1996). All boas, vipers, and some skinks and chameleons are viviparous, as are temperate climate species such as the European lizard (*Lacerta vivipara*), garter snakes (*Thamnophis* spp.), and the slow worm (*Anguis fragilis)*.

Structure of the egg

In contrast to amphibians, which have only the yolk sac, reptile eggs have three membranes and a leathery shell, which though water resistant allows gas exchange. The egg has the amniotic membrane surrounding the embryo, and the chorionic membrane, which covers the inside of the egg. The allantois membrane lies between the two and is attached to the chorion and stores the urea and/or uric acid waste products.

The eggshell is not just a protective layer but also a rich source of calcium to the developing embryo. This is particularly important for turtles, which use 80% of the eggshell to form their shell. All lizards and snakes use their modified tooth (egg tooth) to break their way out of the shell. Chelonians and crocodiles have a horny thickening of the epidermis instead, called the egg caruncle, which performs the same function.

Fat bodies

Fat bodies lie adjacent to the kidney and gonads in the caudal celomic cavity. Some reptiles from temperate climates use these to provide yolk for the first clutch of eggs after the winter. Males show similar cycles but have smaller fat bodies than females.

Maternal care

Some female Indian pythons (e.g., *Python molorus*) show parental care. The female coils around her clutch and generates heat by muscle shivering. This muscle twitching keeps her body temperature 7° C above ambient temperature and may last for up to 2 months. Crocodiles often guard their nest and young for up to a year. However, most reptiles do not exhibit parental care as it poses too much risk to adult survival.

KEY POINTS

- Many chelonia and lizards have temperature dependent sexual determination (TSD).
- Male lizards and snakes have two hemipenes; crocodiles and chelonia have a single phallus.
- Ovarian follicles become heavily filled with yolk from the liver.
- Sperm can be stored for years in the oviduct.

ENDOCRINE SYSTEM

Thyroid gland

Like mammals, thyroid hormones maintain and stimulate metabolism under pituitary control. However, it is only effective in increasing metabolism if temperatures are suitable for that species. It also plays an important role in shedding and growth. In chelonia and snakes, this gland is unpaired and spherical and lies ventral to the trachea just cranial to the heart. In lizards the thyroid varies between species and can be paired, bilobed or unpaired. The commonest is the bilobed organ with an isthmus over the trachea, as in mammals.

Parathyroid glands

The parathyroids have a similar structure to those found in mammals but, unlike them, in reptiles they are found near the thymus or ultimobranchial bodies and not with the thyroids. Chelonia have two pairs; the rostral pair are hard to visualize because they lie within the thymus gland but the caudal pair can be clearly seen near the aortic arch (Clark 1970).

In snakes the rostral pair of parathyroid glands lie near the angle of the jaw, with the second pair lying more caudally, near the thymus and heart. Lizards may have 1–2 pairs depending on the species. A rostral pair lies in the neck near the bifurcation of the carotid arteries and the caudal pair (when present) lie just behind them near the aortic arch (Clark 1970).

The parathyroids control calcium and phosphorous levels. Reptiles on a low calcium diet develop hypocalcemia, which stimulates increased production of PTH. This acts to mobilize calcium from the bones to increase serum calcium. Nutritional secondary hyperparathyroidism and osteopenia eventually results and can be seen clearly on radiographs (Figs. 2.5 and 2.6).

Adrenal glands

These are yellow/red in color and lie retroperitoneally in crocodiles and chelonia and closely adherent to the gonads in lizards and snakes. However, they always lie dorsal to the gonads and, except in chelonia, lie asymmetrically with the right cranial to the left (Gabe 1970).

Chelonia have dorsoventrally flattened glands which lie against the kidney. Ventrally they are covered by peritoneum that extends forward to form the mesorchium or mesovarium of the adjacent gonads. Snakes and lizards have adrenal glands actually incorporated into the mesorchium or mesovarium, close to their respective gonads. They are elongated in snakes and usually globular in lizards. The right gland is attached to the caudal vena cava (Gabe 1970).

Pancreas

This forms a c-shaped loop in chelonia, attached to the mesenteric border of the duodenal loop. In lizards it has three parts: one extending toward the gall bladder, one toward the duodenum, and one toward the spleen.

In snakes the pancreas is often pyramidal in shape and lies caudal to the spleen in the first part of the duodenum. Its location can vary with species but it is often intimately associated with the spleen (Miller & Lagios 1970).

Pineal gland

The pineal gland is closely associated with the parietal eye. It is a saccular organ lined by epithelial cells containing photoreceptor and secretory-like cells. It converts photic stimuli into neuroendocrine messages and may play a role in thermoregulation. Some lizards have a more superficial parietal gland or third eye, which has a lens, cornea, and retina and is located just beneath the skin in the parietal foramen at the junction between the parietal and frontal bone. Although it does not form images, it is thought to sense changes in the intensity and wavelength of light and may aid thermoregulatory shuttling (Bellairs 1969e; Firth & Turner 1982). Crocodiles lack both parietal and pineal glands.

NERVOUS SYSTEM

The reptile is the first group of vertebrates to have 12 cranial nerves (Barten 1996; Bennett, RA 1996). The brain comprises 1% of body mass and is larger than amphibians and fishes, with more developed optic lobes reflecting their well-developed vision. Unlike mammals the spinal cord extends to the tail tip and there is no cauda equina (Bennett, RA 1996). Reptiles do not have a true subarachnoid space; the space between the leptomeninges (pia-arachnoid) and the dura mater is called the subdural space.

CLINICAL NOTE

The spinal cord possesses some localized autonomy so spinal cord injuries could have a better clinical prognosis than in mammals (Bennett, RA 1996).

Senses

Hearing

Crocodiles are the only reptiles with an external ear. In the other species the tympanic membrane is the outer boundary of the middle ear and often lies level with and covered by modified skin. Some species, such as snakes, tuatara, and chameleon, lack a tympanic membrane. Crocodiles, geckos, and turtles have the best hearing of all reptiles (Young 1997).

There is only one single middle ear bone, the *columella*, which is the forerunner of the mammalian stapes and so named because it is column or rod shaped. (In mammals the quadrate and articular bones have become the incus and malleus and this sound conduction system gives mammals better hearing.) The columella is attached to the tympanic membrane and also to the quadrate bone of the lower jaw. Vibrations pass from the air or ground to the tympanic membrane and then to the columella, which then moves the perilymphatic fluid to give rise to nerve impulses (Murray 1996b; Young 1997).

A short, broad auditory (eustachian) tube leads from the middle ear to the pharynx and, as in birds, is not closed. The middle ear is lined by mucous membrane which is continuous with this tube and pharynx. The inner ear consists of the organs of balance: the three semicircular canals, the utricle and saccule, and the organ of hearing, the cochlea. The cochlear duct is not coiled as it is in mammals (Baird 1970; Bellairs 1969e).

Taste and touch

Reptiles have taste buds on their tongue and oral epithelium. Tactile papillae are found along the head and oral cavity in some species. Tactile stimuli play a major role in courtship in snakes and lizards (Young 1997).

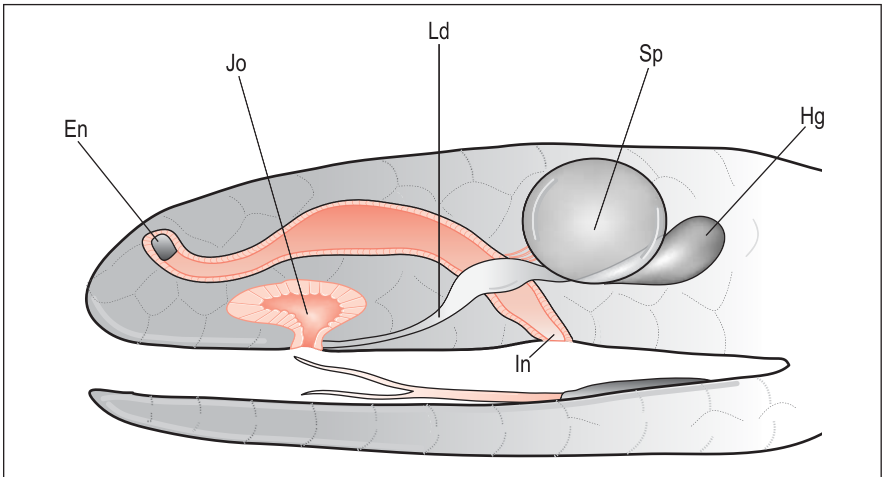
Olfaction

Olfaction plays an important role in courtship and mating. All reptiles have an accessory olfactory organ called Jacobson's organ. These organs are paired and lie on the rostral roof of the oral cavity over the vomer bones. They are lined by thick sensory epithelium and innervated by the vomeronasal nerve, a branch of the olfactory nerve.

Jacobson's organ is most highly developed in snakes (Fig. 2.14) where they receive data from the tip of the tongue as it flickers in and out. Chelonians only have a modified Jacobson's organ while in adult crocodiles it only exists in the early embryonic stage (Bellairs 1969e; Parsons 1970; Young 1997).

Sight

The principal receptors in reptiles are eyes and the secondary receptors are the pineal gland and, possibly, the skin. Lizards and chelonians have scleral ossicles and all eyes have lenses. Aquatic species have poor accommo-



En = External nostril
Hg = Harderian gland
In = Internal nostril
Jo = Jacobson's organ
Ld = Lacrimal duct
Sp = Spectacle

Figure 2.14 • Section of snake head showing the fused eyelids or spectacle, Jacobson's organ and tongue.

dation because the refractive index of water is almost the same as that of the cornea; marine turtles have a very flattened cornea. As in birds, the iris is controlled by skeletal muscle so is non-responsive to mydriatics like atropine. Mydriatics such as *d*-tubocurare can be used instead of general anesthesia (Barten 1996; Bennett, RA 1996; Williams 1996). Miosis is quite sluggish in reptiles and there is no consensual pupillary light reflex. Two large glands are associated with the orbit and these are the Harderian and lacrimal glands.

INTEGUMENT

Although it is commonly thought that reptiles have 'slimy skin' in fact, the converse is true as the skin is dry and has far fewer glands than either amphibians or mammals. It is also heavily keratinized with a lipid layer to prevent water loss. The only glandular-type tissues are the femoral and precloacal pores seen in some lizards, which have a pheromonal function and are better developed in the male (Bellairs 1969d; Lillywhite & Maderson 1982).

The epidermis is both thick and thin in order to form scales and it is these scales that make reptile skin a poor insulator of heat. Unlike fish scales, which can be scraped off, these scales are an integral part of the skin. The scales provide protection from abrasion, play a role in permeability, and tend to be thicker dorsally than ventrally. In some species they are developed into large plates and shields on the head. In snakes they are widened ventrally to form what are called *gastropeges* that are important for locomotion.

CLINICAL NOTE

Skin permeability increases when the skin is in contact with water, so water baths (Fig. 2.15) are a good way of hydrating sick reptiles and treating dysecdysis (Lillywhite & Maderson 1982).

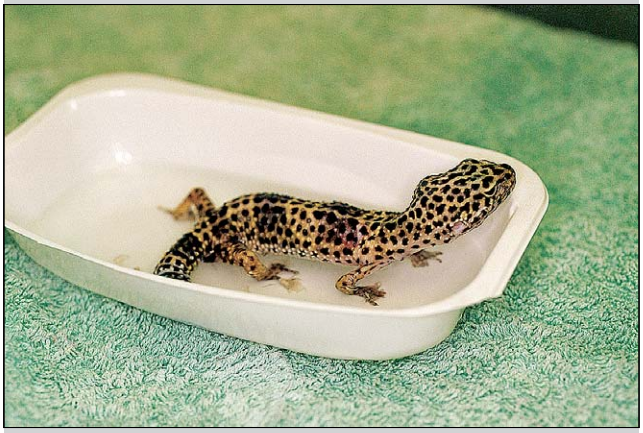


Figure 2.15 • Leopard gecko (*Eublepharis macularius*) being treated in a water bath.

CLINICAL NOTE

Wound healing is slow in reptiles so stitches should be left in for at least 6 weeks (Bennett & Mader 1996; Rossi 1996). It is best to leave stitches in place until ecdysis occurs since the increased activity in the dermis and epidermis promotes better healing and strength.

Epidermis

The epidermis has three layers. The inner layer is called the *stratum germinatum* and consists of cuboidal cells that produce the protein keratin and the dividing cells of the intermediate layer. The intermediate layer has a lipid rich film that plays a major role in providing a water-permeable barrier in the skin. The outer *stratum corneum* is heavily keratinized into the scales. Two forms of keratin are produced in reptiles: alpha-keratin, which is flexible, and beta-keratin, which provides strength and hardness and is unique to reptiles (Fig. 2.16). Beta-keratin is found in the scales of the chelonian shells whereas the alpha-keratin is found in the hinges or between the scutes (Bellairs 1969d; Harvey-Clark 1997; Lillywhite & Maderson 1982). It is at these weaker links that mites or infection like shell rot can be found (Harvey-Clark 1997).

CLINICAL NOTE

The thick, keratinized skin of reptiles is at the expense of cutaneous sensation. Reptiles have far less sensory feeling in their skin than birds or mammals, which is why they are at more risk from thermal burns in captivity.

Dermis

The dermis consists of connective tissue, blood and lymphatic vessels, nerves, and pigment cells. In some species the dermis has bony plates called osteoderms. In chelonians this has fused with the vertebrae to form a shell.

Ecdysis

Ecdysis is the shedding of skin and is controlled by the thyroid gland. Changes in feeding behavior and activity occur prior to ecdysis and the reptiles become very susceptible to dehydration. Snakes tend to shed the whole skin, unlike lizards and chelonians which shed piecemeal, and this makes them even more vulnerable during ecdysis. In a healthy snake the whole process can take up to about 2 weeks.

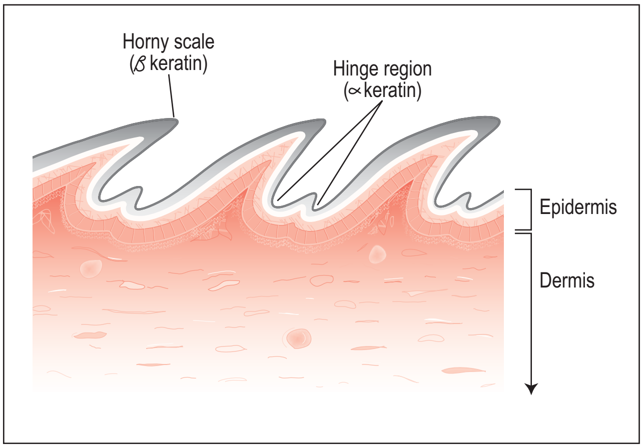


Figure 2.16 • Vertical section through the horny scales of lizard or snake showing hinges between the scales. The hinges are made from the flexible alpha keratin while the beta keratin, which is unique to reptiles, gives strength and hardness to the scales.

During ecdysis the cells in the intermediate layer replicate to form a new three-layer epidermis. Once this process is complete, lymph diffuses into the area between the two layers and enzymes are released to form a cleavage zone. The old skin is shed and the new epithelium hardens, decreasing permeability to become the new skin (Harvey-Clark 1997; Lillywhite & Maderson 1982; Rossi 1996).

CLINICAL NOTE

During ecdysis the skin becomes more permeable and more vulnerable to parasites and infection. Malnourished animals are hypoproteinemic and unable to produce enough enzymes to form a true cleavage zone, resulting in dysecdysis (failure to shed). Lack of moisture will also delay the process (Lillywhite & Maderson 1982).

The production of color

Reptiles have pigment-containing cells called chromatophores that lie between the dermis and epidermis. These not only help in camouflage and sexual display but in thermoregulation. These pigment cells are not just confined to skin but can occur in the peritoneum in some species.

Melanophores produce the pigment melanin and lie deepest in the subepidermal layer. These melanin cells give rise to black, brown, yellow and gray coloration. Albinism in reptiles is caused by lack of melanin. The carotenoid cells are found beneath the epidermis above the melanophores and produce yellow, red and orange pigments (Bellairs 1969d).

Structural colors

The iridophores (guanophores) also lie in the dermis. These contain a semicrystalline product guanine (the breakdown product of uric acid) that reflects light. The blue wavelengths are reflected more to produce a blue color in an effect called Tyndall scattering. When combined with the yellow carotenoids this gives the color green, which is a common camouflage color in many reptiles (Bellairs 1969d).

Iridescence

Iridescence is caused by the physical properties of light on the thin and transparent outer layer of skin. When light strikes it from an angle the light spectrum is split into wavelengths of different colors. Depending on the color of the scales this will cause an iridescent effect when the snake moves. This feature is more obvious in black or dark snakes like the rainbow boa (*Epicrates cenchria*).

KEY POINTS

- The adrenal glands are intimately associated with the gonads in snakes and lizards.
- Reptiles have only one middle ear bone so their hearing is not acute like mammals.
- Jacobson's organ is very well developed, especially in snakes, and plays a major role in olfaction.
- There is no consensual pupillary light reflex and the pupil is non responsive to atropine.
- Reptilian skin has few glands but has a lipid layer to prevent water loss.
- Sick animals suffer from dysecdysis due to lack of moisture and malnutrition.

REFERENCES

Baird, I. L. (1970) The anatomy of the reptilian ear. In C. Gans (ed.), *Biology of the reptilia*. Vol. 2, Morphology B. London: Academic Press. pp. 193–272.

Barten, S. L. (1996) Biology – lizards. In D. R. Mader (ed.), *Reptile medicine and surgery*. Philadelphia: WB Saunders. pp. 47–61.

Bartholomew, G. A. (1982) Physiological control of body temperature. In C. Gans & F. H. Pough (eds.), *Biology of the reptilia*. Vol. 12, Physiology C. London: Academic Press. pp. 167–204.

Bellairs, A. (1969a) *The life of reptiles*. Vol. 1. London: Weidenfeld and Nicolson. Body form, skeleton and locomotion; pp. 44–116.

Bellairs, A. (1969b) *The life of reptiles*. Vol. 1. London: Weidenfeld and Nicolson. Feeding and cranial mechanics; pp. 116–184.

Bellairs, A. (1969c) *The life of reptiles*. Vol. 1. London: Weidenfeld and Nicolson. The internal economy; pp. 217–282.

Bellairs, A. (1969d) *The life of reptiles*. Vol. 2. London: Weidenfeld and Nicolson. The skin; pp. 283–332.

Bellairs, A. (1969e) *The life of reptiles*. Vol. 2. London: Weidenfeld and Nicolson. Nervous system, psychology and sex organs; pp. 332–390.

Bellairs, A. (1969f) *The life of reptiles*. Vol. 2. London: Weidenfeld and Nicolson. Sex and reproduction; pp. 390–433.

Bennett, A. F. (1972) The effect of activity and oxygen consumption, oxygen debt and heart rate in lizards *Varanus gouldii* and *Sauromalus hispidis*. *Journal of Comparative Physiology 79*, 259–280.

Bennett, A. F., & Dawson, W. R. (1976) Metabolism. In C. Gans & W. R. Dawson (eds.), *Biology of the reptilia*. Vol. 5, Physiology A. London: Academic Press. pp. 127–211.

Bennett, A. F., & Nagy, K. A.(1977) Energy expenditure in free ranging lizards. *Ecology 58*, 698–700.

Bennett, R. A. (1996) Neurology. In D. R. Mader (ed.), *Reptile medicine and surgery*. Philadelphia: WB Saunders. pp. 141–148.

Bennett, R. A., & Mader, D. R. (1996) Soft tissue surgery. In D. R. Mader (ed.), *Reptile medicine and surgery*. Philadelphia: WB Saunders. pp. 287–298.

Bentley, P. J. (1976) Osmoregulation. In C. Gans & W. R. Dawson (eds.), *Biology of the reptilia*. Vol. 5, Physiology A. London: Academic Press. pp. 356–408.

Bockman, D. E. (1970) The thymus. In C. Gans & T. Parsons (eds.), *Biology of the reptilia*. Vol. 3, Morphology C. London: Academic Press. pp. 111–114.

Boyer, T. H. (1996) Metabolic bone disease. In D. R. Mader (ed.), *Reptile medicine and surgery*. Philadelphia: WB Saunders. pp. 385–392.

Campbell, T. W. (1996) Clinical pathology. In D. R. Mader (ed.), *Reptile medicine and surgery*. Philadelphia: WB Saunders. pp. 248–257.

Carroll, R. L. (1969) Origin of reptiles. In C. Gans (ed.), *Biology of the reptilia*. Vol. 1. Morphology A. London: Academic Press. pp. 1–40.

Clark, N. B. (1970) The parathyroid. In C. Gans & T. Parsons (eds.), *Biology of the reptilia*. Vol. 3, Morphology C. London: Academic Press. pp. 235–247.

Dantzler, W. H. (1976) Renal Function (with special emphasis on nitrogen excretion). In C. Gans & W. R. Dawson (eds.), *Biology of the reptilia*. Vol. 5, Physiology A. London: Academic Press. pp. 447–496.

Davis, L. E., Schimdt-Nielson, B., & Stolte, H. (1976) Anatomy and ultrastructure of the excretory system of the lizard, *Sceloporus cyanogenys*. *Journal of Morphology 149*, 279–326.

DeNardo, D. (1996) Reproductive biology. In D. R. Mader (ed.), *Reptile medicine and surgery*. Philadelphia: WB Saunders. pp. 212–224.

Dunson, W. A. (1976) Salt glands in reptiles. In C. Gans & W. R. Dawson (eds.), *Biology of the reptilia*. Vol. 5, Physiology A. London: Academic Press. pp. 413–441.

Edmund, A. G. (1970) Dentition. In C. Gans (ed.), *Biology of the reptilia*. Vol. 1, Morphology A. London: Academic Press. pp. 117–194.

Enlow, D. H. (1970) The bone of reptiles. In C. Gans (ed.), *Biology of the reptilia*. Vol. 1, Morphology A. London: Academic Press. pp. 45–77.

Espinoza, R. E., & Tracy, C. R. (1997) Thermal biology, metabolism and hibernation. In L. Ackermann (ed.), *The biology, husbandry and healthcare of reptiles*. Vol. 1, The biology of reptiles. TFH Publications, N.J. pp. 149–184.

Evans, H. E. (1986) Reptiles – Introduction and anatomy. In M. E. Fowler (ed.), *Zoo and wild animal medicine*, 2nd edn. Philadelphia: WB Saunders. pp. 108–132.

Firth, B. J. & Turner, J. S. (1982) Sensory, neural and hormonal aspects of thermoregulation. In C. Gans & F. H. Pough (eds.), *Biology of the reptilia*. Vol. 12, Physiology C. London: Academic Press. pp. 213–259.

Fox, H. (1977) The urogenital system of reptiles. In C. Gans & T. Parsons (eds.), *Biology of the reptilia*. Vol. 6, Morphology E. London: Academic Press. pp. 1–122.

Gabe, M. (1970) The adrenals. In C. Gans & T. Parsons (eds.), *Biology of the reptilia*. Vol. 3, Morphology C. London: Academic Press. pp. 268–275.

Gans, C. & Hughes, G. M. (1967) The mechanism of lung ventilation in the tortoise *Testudo Graeca Linne*. *Journal of Experimental Biology 47*, 1–20.

Gregory, P. T. (1982) Reptilian hibernation. In C. Gans (ed.), *Biology of the reptilia*. Vol. 13, Physiology D. London: Academic Press. pp. 53–140.

Haines, R. W. (1970) Epiphyses and sesamoids. In C. Gans (ed.), *Biology of the reptilia*. Vol. 1, Morphology A. London: Academic Press. pp. 81–112.

Harvey-Clark, C. J. (1997) Dermatologic (skin) disorders. In L. Ackermann (ed.), *The biology, husbandry and healthcare of reptiles*, Vol. 3. TFH Publications, N.J. pp. 654–658.

Hoffstetter, R., & Gasc, J. P. (1970) Vertebrae and ribs of modern reptiles. In C. Gans (ed.), *Biology of the reptilia*. Vol. 1, Morphology A. London: Academic Press. pp. 201–302.

Holz, P. H. (1999) The reptilian renal-portal system: Influence on therapy. In M. E. Fowler & R. E. Miller (eds.), *Zoo and wild animal medicine: Current therapy*, 4th edn. Philadelphia: WB Saunders. pp. 249–252.

King, G. (1996a) *Reptiles and herbivory*. London: Chapman & Hall. Reptiles and herbivory, C; pp. 1–23.

King, G. (1996b) *Reptiles and herbivory*. London: Chapman & Hall. Lizards; pp. 29–42.

King, G. (1996c) *Reptiles and herbivory*. London: Chapman & Hall. Turtles and tortoises; pp. 47–60.

King, G. M. & Custance, D. R. (1982) *Colour atlas of vertebrate anatomy*. Oxford: Blackwell Scientific. The lizard; pp. 4.1–4.10.

Lichtenbelt, W. D. (1992) Digestion in an ectotherm herbivore, the green iguana (Iguana): Effect of food composition and body temperature. *Physiological Zoology 65*(3), 649–673.

Liem, K. F., Bemis, W. E., Walker, W. F., & Grande, L. (eds.) (2001) *Functional anatomy of the Vertebrates*, 3rd edn. Fort Worth, Tex.: Harcourt College. Respiration; pp. 591–593.

Lillywhite, H. B., & Maderson, P. F. (1982) Skin structure and permeability. In C. Gans & F. H. Pough (eds.), *Biology of the reptilia.* Vol. 12, Physiology C. London: Academic Press. pp. 397–433.

Mader, D. R. (ed.) (1996) *Reptile medicine and surgery*. Philadelphia: WB Saunders. Gout; pp. 374–379.

McCutcheon, F. H. (1943) The respiratory mechanism in turtles. *Physiological Zoology 16*, 255–269.

Miller, M. R., & Lagios, M. D. (1970) The pancreas. In C. Gans & T. Parsons (eds.), *Biology of the reptilia.* Vol. 3, Morphology C. London: Academic Press. pp. 320–324.

Minnich, J. E. (1982) The use of water. In C. Gans & F. H. Pough (eds.), *Biology of the reptilia.* Vol. 12, Physiology C. London: Academic Press. pp. 325–386.

Murray, M. J. (1996a) Cardiology and circulation. In D. R. Mader (ed.), *Reptile medicine and surgery*. Philadelphia: WB Saunders. pp. 95–104.

Murray, M. J. (1996b) Aural abscess. In D. R. Mader (ed.), *Reptile medicine and surgery*. Philadelphia: WB Saunders. pp. 349–352.

Murray, M. J. (1996c) Pneumonia and normal respiratory function. In D. R. Mader (ed.), *Reptile medicine and surgery*. Philadelphia: WB Saunders. pp. 396–405.

Ottaviani, G., & Tazzi, A. (1977) The lymphatic system. In C. Gans & T. Parsons (eds.), *Biology of the reptilia.* Vol. 6, Morphology E. London: Academic Press. pp. 315–458.

Palmer, B., Uribe, M. C., et al. (1997) Reproductive anatomy and physiology. In L. Ackermann (ed.), *The biology, husbandry and healthcare of reptiles*. Vol. 1, The biology of reptiles. N.J.: TFH Publications. pp. 54–81.

Parsons, T. S. (1970) The nose and Jacobson's organs. In C. Gans (ed.), *Biology of the reptilia.* Vol. 2, Morphology B. London: Academic Press. pp. 99–185.

Perry, S. F. (1989) Structure and function of the reptilian respiratory system. In S. C. Wood (ed.), *Comparative pulmonary physiology – current concepts*. New York: Dekker. pp. 193–237.

Perry, S. F., & Duncker, H. R. (1978) Lung architecture, volume and static mechanics in five species of lizards. *Respiratory Physiology 34*, 61–81.

Pough, F. H., Andrew, R. M., Cadle, J. E. et al. (1998a) *Herpetology*. Englewood Cliffs, N.J: Prentice Hall. Herpetology as a field of study; pp. 1–20.

Pough, F. H., Andrew, R. M., Cadle, J. E. et al. (1998b) *Herpetology*. Englewood Cliffs, N.J: Prentice Hall. Classification and diversity of extant reptiles; pp. 75–133.

Pough, F. H., Andrew, R. M., Cadle, J. E. et al. (1998c) *Herpetology*. Englewood Cliffs, N.J: Prentice Hall. Temperature and water relations; pp. 137–172.

Pough, F. H., Andrew, R. M. Cadle, J. E. et al. (1998d) *Herpetology*. Englewood Cliffs, N.J: Prentice Hall. Energetics and performance; pp. 173–204.

Pough, F. H., Andrew, R. M., Cadle, J. E. et al. (1998e) *Herpetology*. Englewood Cliffs, N.J: Prentice Hall. Reproduction and life history; pp. 204–235.

Pough, F. H., Andrew, R. M., Cadle, J. E. et al. (1998f) *Herpetology*. Englewood Cliffs, N.J: Prentice Hall. Feeding; pp. 267–305.

Pough, F. H., Janis, C. M., & Heiser, J. B. (2002a) *Vertebrate life*, 6th edn. Englewood Cliffs, N.J: Prentice Hall. Turtles; pp. 270–294.

Pough, F. H., Janis, C. M., & Heiser, J. B. (2002b) *Vertebrate life*, 6th edn. Englewood Cliffs, N.J: Prentice Hall. The lepidosaurs: Tuatara, lizards and snakes; pp. 294–341.

Redrobe, S., & MacDonald, J. (1999) Sample collection and clinical pathology of reptiles. In D. R. Reavill (ed.), *Clinical pathology and sample collection.* The Veterinary Clinics of North America: Exotic animal practice. Vol. 2. Philadelphia: WB Saunders. pp. 709–730.

Roberts, J. A. B, & Lillywhite, H. B. (1980) Lipid barrier to water exchange in reptile epidermis. *Science 207*, 1077–1079.

Rossi, D. I. V. (1996) Dermatology. In D. R. Mader (ed.), *Reptile medicine and surgery*. Philadelphia: WB Saunders. pp. 104–117.

Secor, S. M., & Diamond, J. (1995) Adaptive responses to feeding Burmese Pythons: Pay before pumping. *Journal of Experimental Biology 198*, 1313–1325.

Secor, S. M., & Nagy, K. A. (1994) Energetic correlates of foraging mode of snakes *Crotalus cerastes* and *Masticophis flagellum*. *Ecology 75*, 1600–1614.

Seymour, R. S. (1982) Physiological adaptations to aquatic life. In C. Gans (ed.), *Biology of the reptilia.* Vol. 13, Physiology D. London: Academic Press. pp. 1–41.

Skoczylas, R. (1978) The physiology of the digestive tract. In C. Gans & K. A. Gans (eds.), *Biology of the reptilia.* Vol. 8, Physiology B. London: Academic Press. pp. 589–658.

Thompson, M. B.(1997) Egg physiology and biology. In L. Ackermann (ed.), *The biology, husbandry and healthcare of reptiles*. Vol. 1, The biology of reptiles. N.J.: TFH Publications. pp. 88–121.

Troyer, K. (1984) Structure and function of the digestive tract of a herbivorous lizard *Iguana iguana*. *Physiological Zoology 57*(1), 1–8.

Uetz, P. (2000) How many reptile species? *Herpetology Review 31*, 13–15.

White, F. N. (1976) Circulation. In C. Gans & W. R. Dawson (eds.), *Biology of the reptilia.* Vol. 5, Physiology A. London: Academic Press. pp. 275–328.

Williams, D. L. (1996) Opthalmology. In D. R. Mader (ed.), *Reptile medicine and surgery*. Philadelphia: WB Saunders. pp. 175–185.

Wood, S. C., & Lenfant, C. J. (1976) Respiration: Mechanics, control and gas exchange. In C. Gans & W. R. Dawson (eds.), *Biology of the reptilia.* Vol. 5, Physiology A. London: Academic Press. pp. 225–267.

Young, B. A. (1997) Hearing, taste, tactile reception and olfaction. In L. Ackermann (ed.), *The biology, husbandry and healthcare of reptiles*. Vol. 1, The Biology of reptiles. N.J.: TFH Publications. pp. 185–213.

3

Tortoises and turtles

INTRODUCTION

Chelonians (along with the tuatara) are the most ancient of all living reptiles and evolved over 200 million years ago (Evans 1986). They predate dinosaurs and their primeval shelled appearance has made them a popular and fascinating pet with none of the sinister connotations of snakes. Their survival through evolution is related to their ability to withdraw their head inside the protective armor of their shell. Consequently, they have not needed to diversify, which is why flying and fossorial turtles do not exist (King 1996).

North America has a quarter of the world's chelonians (Evans 1986) while Europe has only two species of freshwater turtle and three terrestrial species. Australia has no terrestrial species and only has aquatic sidenecks.

Longevity

Of all the reptiles, chelonians live the longest, with many living well over 50 years in captivity. Larger species like the Galapagos tortoise (*Geochelone nigra*) have been recorded to live for over 150 years (Bellairs 1969d; Pough et al. 1998a, 2002).

Size

The largest chelonia are the marine Leathery turtle (*Dermochelys coriacea*), which can weigh 680 kg and the Galapagos Giant tortoise weighing 263 kg. Larger size does confer the advantage of thermal inertia and the ability to store fat for lean periods. The majority of species reach a maximum carapace length of 30 cm although smaller species like the Madagascar Spider tortoise (*Pyxis arachnoides*) has an adult shell length of only 10 to 15 cm (Bellairs 1969d).

TAXONOMY

Chelonia have a dramatic ability to flex their cervical vertebrae and are classified into two suborders according to their mode of retracting their head into their shell (Fig. 3.1).

The Pleurodira or sideneck turtles have three main points of neck flexure so the neck forms a horizontal "s" shape. They are more primitive than the Cryptodira, being unable to retract their head inside their shell, instead placing it sideways. These are mainly aquatic or semi-aquatic turtles and are only found in the southern continents.

The Cryptodira or hidden-neck turtles have two points of neck flexure that form a vertical "s" bend, allowing the head to be completely withdrawn inside the shell. This has enabled them to be more successful and includes the majority of chelonian species (11 families). Some species, such as the Snapper turtle and sea turtles, have lost the ability to hide their head in their shell (Bellairs 1969a; Hoffstetter & Gasc 1970; King 1996).

Terminology

Chelonia refers to the order of shelled reptiles. In North America the word "turtle" is the common term for any reptile with a shell, although the term tortoise is used for terrestrial species like the Testudinidae. In other parts of the world different terms may be used according to habitat. Tortoises are land based, terrapins are freshwater semi-aquatic, and the word turtle is reserved solely for marine and aquatic species (Table 3.1).

THERMOREGULATION

Chelonians are heliotherms (Boyer & Boyer 1996), with a temperature range from 22 to 33° C. Many smaller species bask in the sun to heat up. They have difficulty cooling down, owing to their shell, so seek shade by burrowing under vegetation. Large chelonians in arid deserts find it difficult to reach shade because of their large size, so they lose heat by evaporative cooling. They achieve this by hypersalivating or urinating on their legs and plastron (Bartholomew 1982).

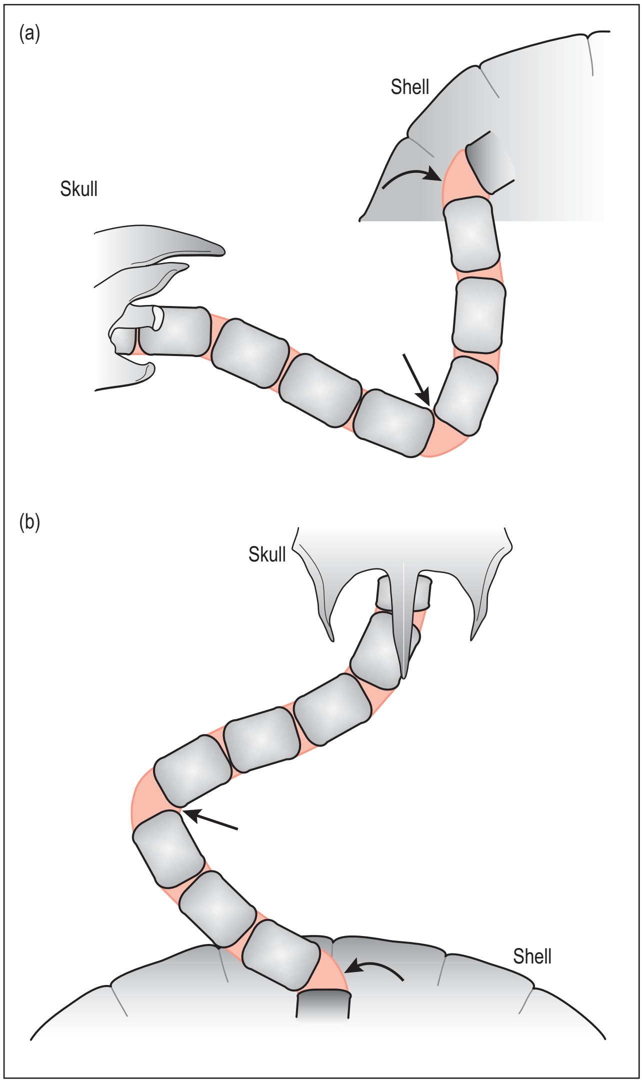


Figure 3.1 • Neck flexure in chelonian (*arrows* indicate point of maximum flexure).
(a) Cryptodires showing neck flexure from the side
(b) Pleurodires showing neck flexure from above

Hibernation

Chelonians from subtropical or temperate areas hibernate in winter months under the influence of decreasing temperatures. Terrestrial species bury themselves below the frostline underground while some aquatic species bury themselves in mud at the bottom of a pond where water is so dense it does not freeze. These latter survive by using anaerobic metabolism and absorbing dissolved oxygen through their skin and pharyngeal mucosa (Gregory 1982).

CLINICAL NOTE

Semi-aquatic turtles, like the Red-eared slider, bask on dry land to aid digestion of food. However, basking in the sun may also play a role in ecdysis and prevents fungal infections by drying out the shell (Pough et al. 2002).

GENERAL EXTERNAL ANATOMY

Anatomical modifications have evolved according to the habitat and whether it is terrestrial, marine, or freshwater.

Terrestrial (tortoises)

These are high-domed, stump-legged, small-headed vegetarians (Fig. 3.3) that are found in hot and arid climates (Evans 1986; Hoffstetter & Gasc 1970; Pough 1998a). They have developed thick skin and large scales to prevent desiccation. Largest of the land tortoises include the Galapagos tortoise (*Geochelone nigra*) (Fig. 3.2) and the Aldabra (*Geochelone gigantea*), but they mainly range from 10 to 120 cm in size. Many smaller species, like the North American Gopher (*Gopherus polyphemus*) tortoise, have adapted for burrowing with a flatter dome and scoop-shaped forelegs, while the African Pancake tortoise (*Malacochersus tornieri*) has a shell so flat and flexible it can slide between rock crevices to escape predators (Pough et al. 2002).

Aquatic

Chelonia are well modified for aquatic existence as they can easily breathhold, and utilize anaerobic metabolism and non-pulmonary respiration through skin, pharynx or cloaca. They also have the ability to shunt blood away from the lungs while diving and tolerate severe acid–base imbalances.

Marine

Marine species are the largest of all and have evolved a flatter, softer shell for better streamlining (Fig. 3.4). The metacarpal/tarsal bones and phalanges are elongated for swimming and are similar to flippers. The fore flippers are long and oar-like and used for propulsion while the hind flippers are used for steering and digging the nest. The Leatherback turtle (*Dermochelys coriacea*) is the largest, the Hawksbill turtle (*Eretmochelys imbricata*) the smallest (Evans 1986; Pough et al. 2002).

Freshwater

These are aquatic or semi-aquatic, have webbed feet and a smooth shell. Softshell turtles (Trionychidae) from North America and Asia are strong swimmers and mainly carnivorous. They are the most aquatic of all freshwater species

Table 3.1 Taxonomy and classification of Chelonia (Pough et al. 1998a, 2002)

Suborder	Family	Location	Examples
Pleurodira	Chelidae	Australasia, S. America	Matamata
	Pelomedusidae	Africa, S. America	River turtle
Cryptodira	Carettochelyidae	Australasia	Pig-snouted river turtle
	Cheloniidae	Marine	Green turtle, Hawksbill turtle
	Chelydridae	North America, Central America	Snapping turtle
	Dermatemydidae	Central America	River turtle
	Dermochelyidae	Marine	Leatherback turtle
	Emydidae	N & S. America, Europe, Asia, Africa	Box, Common slider, European pond terrapin
	Kinosternidae	North America	Mud and musk turtles
	Platysternidae	Southeast Asia	Big-headed turtle
	Staurotypidae	Central America	Mexican musk turtle
	Testudinidae	Cosmopolitan, except Australia	Herman's tortoise, Leopard tortoise
	Trionychidae	N. America, Africa, Asia	Softshell turtles

GENERAL INTEREST

How can a reptile with a heavy shell submerge in water and walk along the bottom?

This is achieved by large lung volume, specific gravity, and stored water.

Semiaquatic turtles, like the Red-eared slider (*Trachemys scripta*) have a specific gravity lighter than water, so they float. Their shell accounts for about 75% of their mass so they also have a larger pulmonary volume and extra buoyancy from their bladder and cloaca. When they dive they expel gas from their lungs to submerge (Wood & Lenfant 1976).

Fully aquatic turtles tend to have a specific gravity slightly greater than water and so they tend to sink and require little effort to stay underwater. They also tend to have flatter shells and less lung volume (Seymour 1982).

and can remain submerged for long periods using their long necks to grab at passing prey. They have a leathery, flat shell, large webbed feet, and reduced plastron to allow for free limb movement and little water resistance (Evans 1986; Pough et al. 2002).

Snapping turtles (Chelydridae) have such a reduced shell that the head can only be retracted into the neck folds, leaving the nose visible (Fig. 3.5). These are not good swimmers and often walk along the bottom of ponds. They are omnivores and have strong jaws for predation and protection (Evans 1986; Pough et al. 2002).

SKELETAL SYSTEM AND INTEGUMENT

Locomotion

Terrestrial chelonian species have limbs that project sideways so the muscles tire easily and progress can be laborious. Despite their awkward gait and the weight of the shell they can, however, move at great speed. Aquatic species have evolved different methods of locomotion. Freshwater turtles swim with alternate beats in a paddling motion and some can walk along the bottom. Marine turtles move their forelimbs in unison like flippers, using their rear limbs like rudders (Walker 1973).

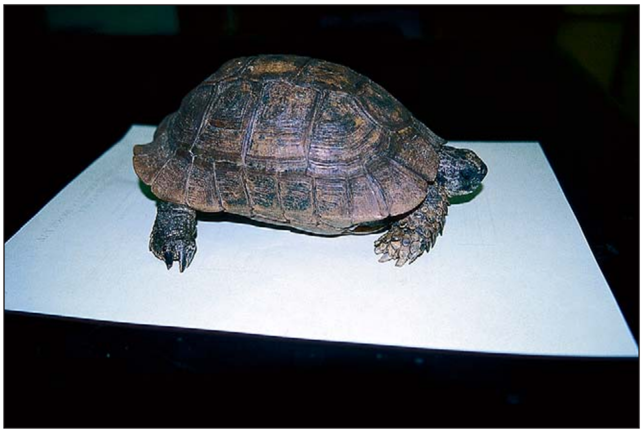
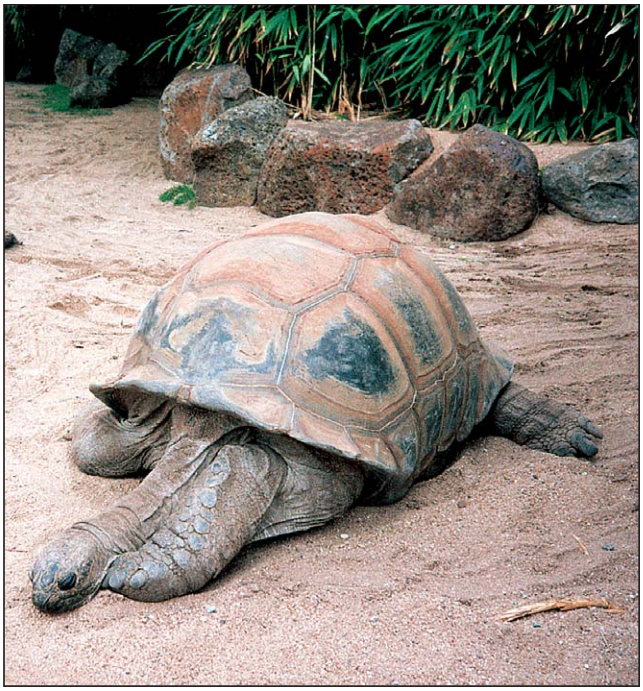


Figure 3.2 • Spur-thigh tortoise (*Testudo graeca*) showing the high domed shell and short, stubby legs of terrestrial species.



Figures 3.3 • Despite its enormous size the Galapagos tortoise (*Geochelone nigra*) has retained a head small enough to retract inside the shell.

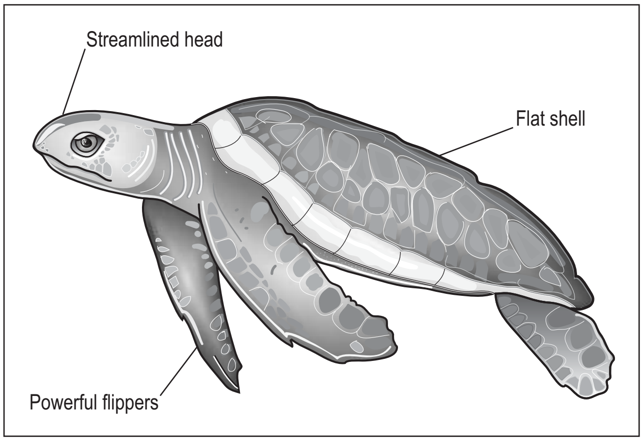


Figure 3.4 • Green sea turtle (*Chelonia mydas*). Marine species have evolved a flatter, softer shell for streamlining with long, fore flippers for powerful propulsion.

The shell

The dome of the shell is called the *carapace* and the flat underpart is called the *plastron*. The joint between the carapace and plastron is called the *bridge*. The cranial aperture is called the *axillary aperture*, and caudally is the *inguinal aperture*. The shell is formed from dermal bone and consists of about 60 bones formed from the modified pectoral and pelvic limb girdles, trunk vertebrae, sacrum, and ribs. These are covered by keratinized epidermal scales known as *scutes* (Fig. 3.14). These scutes do not correspond with the underlying bone, adding greater protection and strength to the shell (Pough et al. 1998a; Zangerl 1970).

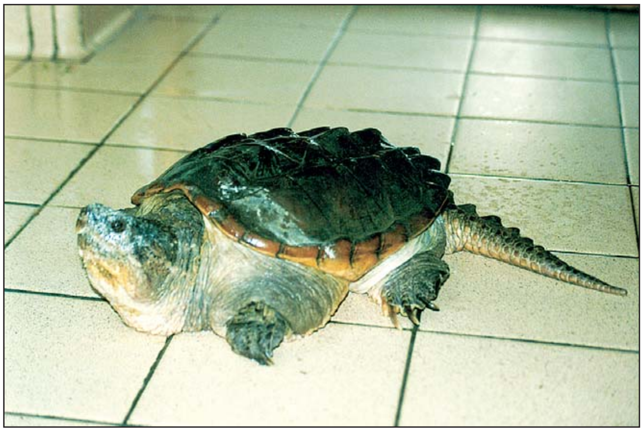


Figure 3.5 • Snapping turtle (*Chelydra serpentina*). The powerful snapping jaws compensate for the inability to retract the head into the shell.

Skeleton

Skull

Chelonians belong to the subclass Anapsida (without arches) because they lack true temporal openings (Fig. 3.6). However, many species do have gaps in the temporal region that provide a pseudotemporal fossa for muscle attachments.

Although the head has to be kept small to enable it to be retracted, the sturdy skull, large adductor muscles, and short jaw still enables chelonians to have a strong bite.

On either side of the small brain case there are large paired supratemporal fossae. Strong retractor muscles extend from these fossae and supraoccipital crest to the base of the neck, enabling them to retract their head. These muscles also enable them to pull at food with their heads while holding it with their limbs (Evans 1986).

In order to keep the head small yet retain a strong bite, the adductor muscles run through a trochlear pulley, which lengthens the muscle fibers and gives them extra strength (Fig. 3.7). In Pleurodira this pulley is formed by a process on the pterygoid bones while in Cryptodira it is formed by the quadrate bones. In each case, although the muscles originate from the back of the skull the muscle is redirected vertically for maximum force (King 1996; Pough et al. 1998a).

Mandible

In Chelonia the mouth opens by lowering the jaw (the reverse of crocodiles). Like lizards, they have a mandibular symphysis, and jaw articulation is between the quadrate bone and the articular bone of the lower jaw.

Vertebrae

There are 18 presacral vertebrae, consisting of 8 cervical and 10 trunk vertebrae. The trunk vertebrae each have rib

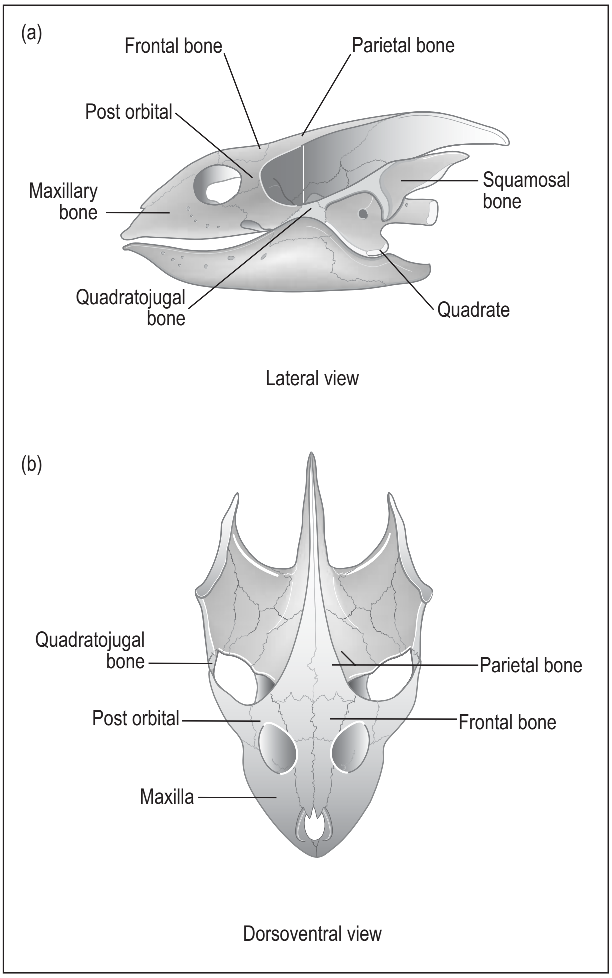

(a)
Frontal bone
Parietal bone
Post orbital
Maxillary bone
Squamosal bone
Quadratojugal bone
Quadrate
Lateral view
(b)
Quadratojugal bone
Parietal bone
Post orbital
Frontal bone
Maxilla
Dorsoventral view

Figure 3.6 • Modified anapsid skull of chelonian.
(a) Lateral view
(b) Dorsoventral view

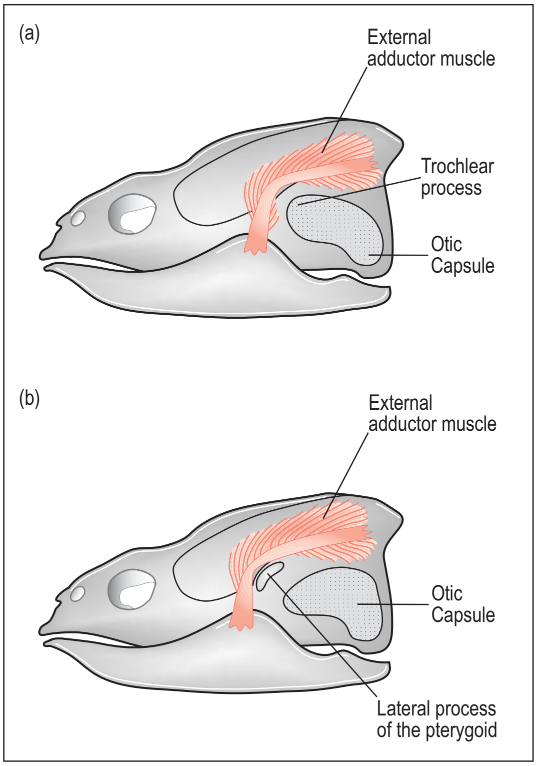

(a)
External adductor muscle
Trochlear process
Otic Capsule
(b)
External adductor muscle
Otic Capsule
Lateral process of the pterygoid

Figure 3.7 • Lateral view of chelonian skull showing adductor muscle pulley system. Redirecting the muscles vertically for maximum force enables the head to be kept small so that it can be drawn in for protection from predators.
(a) Cryptodires – the pulley runs by the quadrate bone
(b) Pleurodires – the pulley runs along the lateral process of the pterygoid bone

attachments which fuse with the dermal bone plates (Figs. 3.8–3.11). There is no sternum. In contrast to the fused trunk, the cervical and caudal vertebrae are free. The neck and tail are highly flexible and have well-developed epaxial and hypaxial muscles (Evans 1986).

Cervical vertebrae

The eight cervical vertebrae allow for bending of the neck sideways (Pleurodira) or inside the shell (Cryptodira). The Pleurodira cannot retract their head entirely inside the shell and this lack of protection may explain why they have been less successful and their range limited to the southern continents.

CLINICAL NOTE

Chelonia are the only tetrapods that have their pectoral and pelvic girdle inside their "ribs". This means that chelonians do not possess an expandable rib cage for breathing.

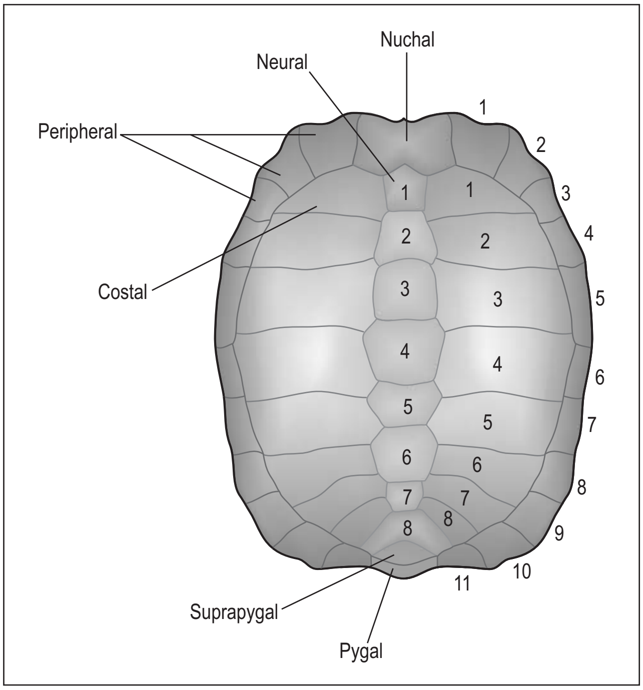

Nuchal
Neural
Peripheral
Costal
Suprapygal
Pygal
1
2
3
4
5
6
7
8
1
2
3
4
5
6
7
8
1
2
3
4
5
6
7
8
9
10
11

Figure 3.8 • Dorsal carapace showing dermal bone plates.

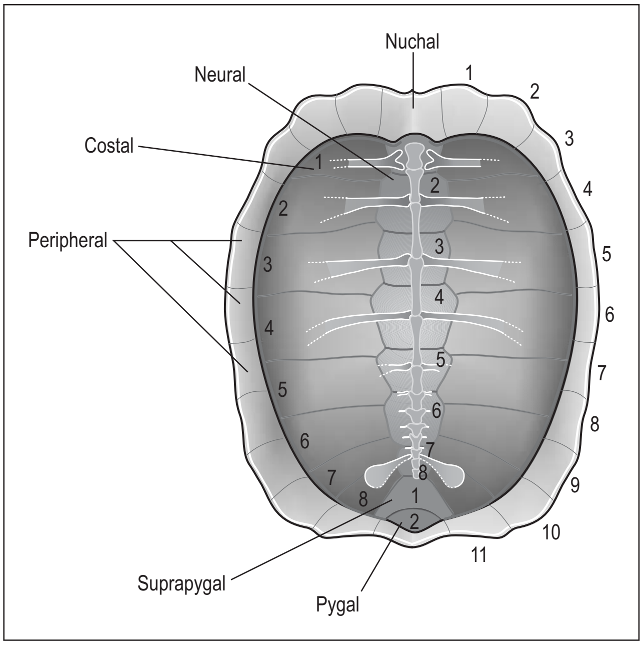


Figure 3.9 • Ventral carapace showing dermal bone plates.

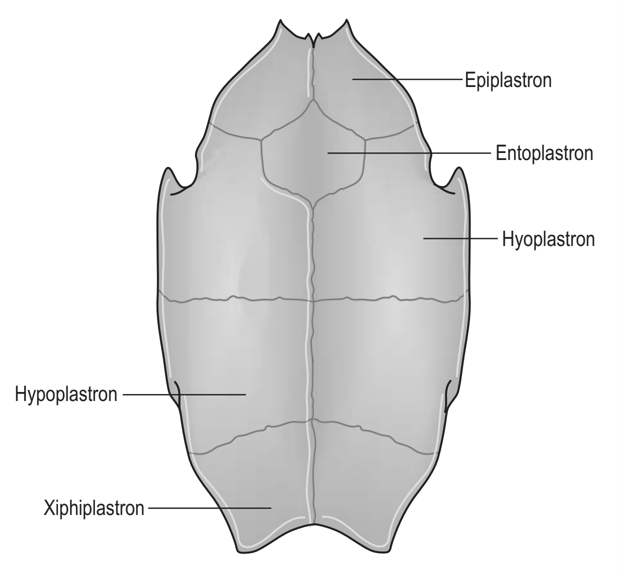


Figure 3.10 • Ventral plastron showing dermal bone plates.

Limb girdles

The pectoral and pelvic girdle both occupy a unique position inside the ribs and act like vertical pillars giving extra strength to the shell. These two bony girdles are attached to the plastron and carapace by fan-shaped pectoral and pelvic muscles. These limb muscles constitute the largest muscle mass and are surprisingly powerful. Fat is deposited between the limb base and the shell, so obese animals could have difficulties withdrawing into their shell and breathing.

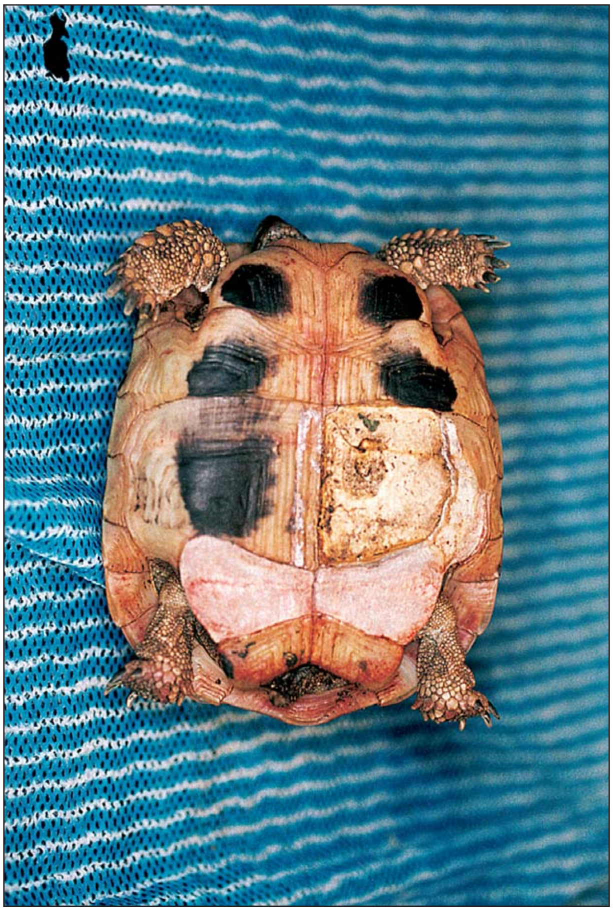


Figure 3.11 • Hermann's tortoise (*Testudo hermanni*) with severe osteomyelitis and septicemia. The femoral and abdominal epidermal scutes have sloughed off to reveal the xiphiplastron and hypoplastron dermal bones beneath.

Pectoral girdle

The pectoral girdle consists of the epiplastron (clavicle), the entoplastron (interclavicle) and a tripartite arrangement of scapula, acromion process and coracoid bone. The scapula fuses dorsally with the carapace via a ligamentous attachment and ventrally articulates with the humerus at the glenoid cavity. A prominent acromion process projects medially, almost touching its counterpart and is fused to the plastron via connective tissue bands. The third strut is the coracoid bone, which extends caudomedially and also articulates with the glenoid fossa (Figs. 3.12 and 3.13) (Bellairs 1969a).

Pelvic girdle

The ilium, ischivin and pubic bones are paired and meet at the acetabulii; the ilium is attached dorsally to the sacral ribs. In Pleurodira the pelvic girdle is fused more strongly to the carapace by the ilia dorsally, and pubic and ischial bones ventrally, leaving the sacral attachment weaker (Hoffstetter & Gasc 1970).

Limbs

The humerus and femur are short in length, with expansion of the proximal and distal extremities. A fused carpus and

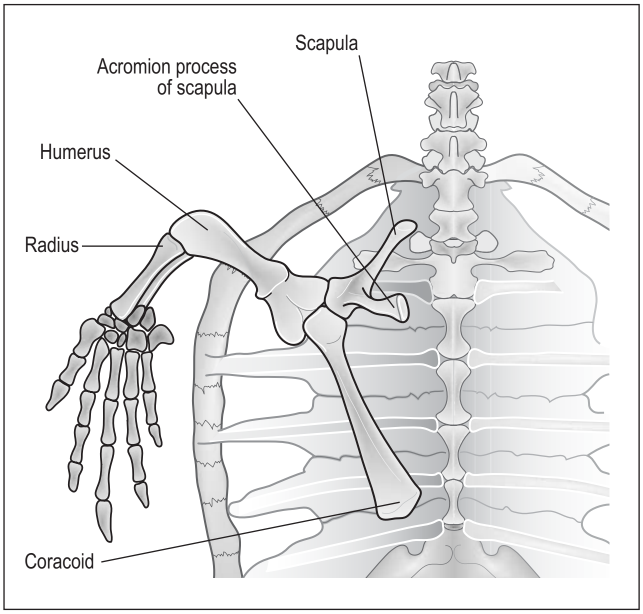


Figure 3.12 • Ventral view of tripartite chelonian shoulder. The scapula fuses dorsally with the carapace via a ligamentous attachment. A prominent acromion process projects medially while the coracoid bone extends caudomedially.

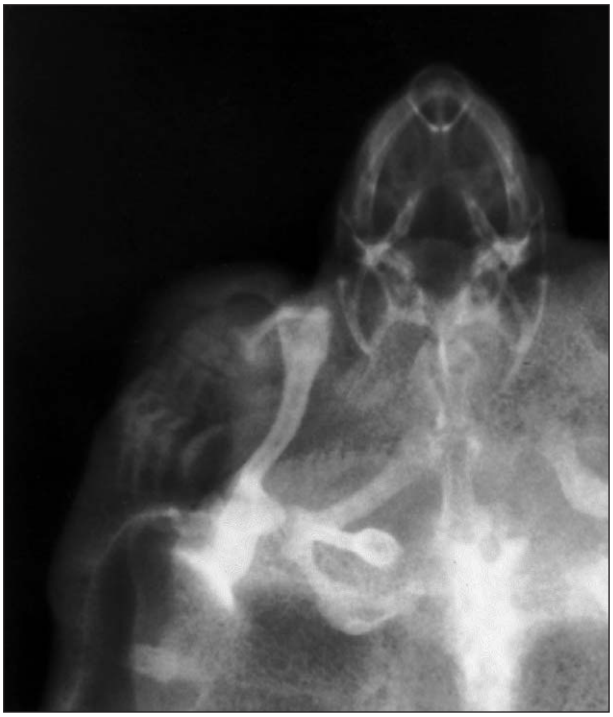


Figure 3.13 • Dorsal view of left shoulder of Red-eared slider (*Trachemys scripta*) showing tripartite shoulder.

tarsus all give added strength. All species have five claws on each foot, except the tortoises, which have short stubby toes and only four claws on the hind feet. The limbs are covered by conventional scales and have strong claws for digging. Freshwater turtles have webbed and flattened feet; the marine turtles have modified their forelimbs into flippers (Walker 1973).

Scutes

The outer part of the shell is covered with horny scutes formed from the epidermis and is the equivalent of scales in other reptiles. The number and size of scutes helps identify the species. The scutes, being of epidermal origin, are innervated and bleed if damaged. Growth occurs by the addition of new keratinized layers to the base of each scute. Greater cell activity around the perimeter of each new layer causes the scutes to widen gradually.

The scutes of the carapace are termed *marginal*, *cervical*, *pleurals* (costals) and *vertebrals* (Fig. 3.15). The scutes of the plastron are called *gular*, *humeral*, *pectoral*, *abdominal*, *femoral*, and *anal* (Fig. 3.16).

CLINICAL NOTE

It would be useful if chelonians could be aged by the ring of new growth in the shell, but as this can be interrupted by changes in food supply, seasonal change, and hibernation in temperate species it does not necessarily correspond with a year's growth (Enlow 1970; Hoffstetter & Gasc 1970).

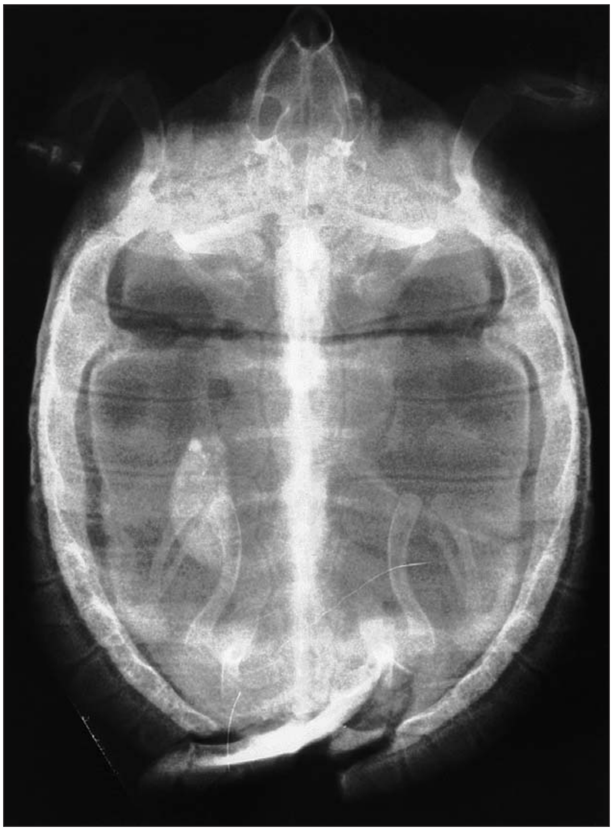


Figure 3.14 • Dorsoventral radiograph of carapace of juvenile Hermann's tortoise (*Testudo hermanni*) with shell fractured by lawn mower.

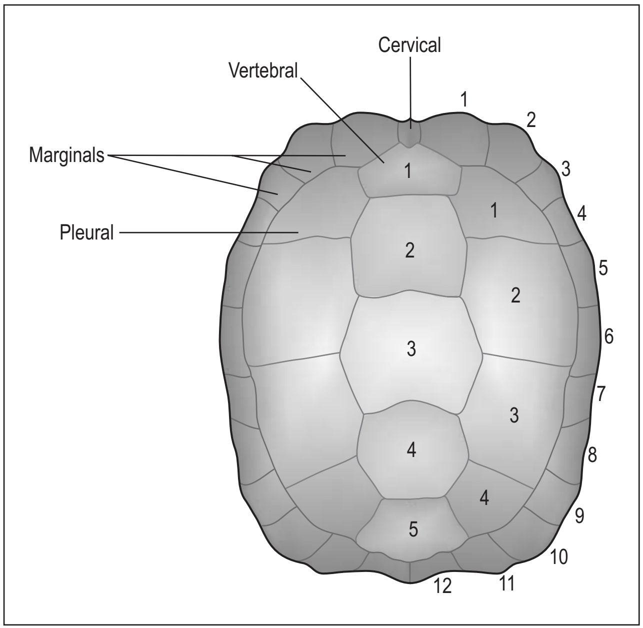


Figure 3.15 • Epidermal scutes of carapace.

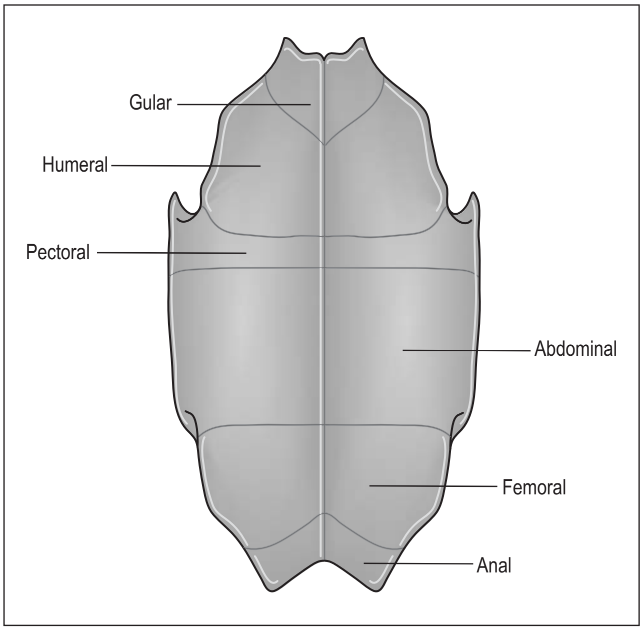


Figure 3.16 • Epidermal scutes of plastron.

Color and patterns

Many male Red-eared sliders (*Trachemys scripta*) go melanistic with age. When young they often have striking yellow plastrons, with clear patterns that become obliterated by pigment as they age (Hoffstetter & Gasc 1970).

Ecdysis

Like all reptiles, chelonians shed their skin but it tends to be in a piecemeal fashion. Aquatic terrapins shed their scutes as they grow, with the old scutes loosening first at the edges and then toward the center.

CLINICAL NOTE

Pyramidal growth of the shell may be caused by excess protein being available during the growing phase.
For example, if herbivorous tortoises are fed on dog food when juvenile this results in excessive growth surges and an imbalance in keratin production.

Shell modifications

Some species, like the Common box turtle (*Terrapene carolina*), have hinges of cartilaginous tissue between the sutures of the bony plates instead of the normal ossified sutures. These enable them to withdraw their head, tail, and limbs and close up like a box. The softshell turtles have leathery skin replacing hard scutes to make them more flexible. Marine species have reduced the bone plates even more, creating a tough, leathery shell for better streamlining. Other species, such as the Common snapping turtle (*Chelydra serpintina*), have such a small shell that they are unable to retract inside their shell at all. They escape predation by being extremely aggressive instead (Pough et al. 2002).

KEY POINTS

- Small head but incredibly strong retractor muscles
- Neck and tail are flexible but rest of spine is fused with shell, rib cage, and plastron
- No expandable rib cage
- Each shoulder is tripartite

CARDIOVASCULAR SYSTEM

The heart lies in the midline, slightly caudal to the pectoral girdle in a pericardial cavity and separate from the cranial part of the ventral body cavity. It is three chambered with an incomplete ventricular septum, although functional pulmonary and systemic circulation is separate. The aortic arches are paired. The left aorta gives rise to a celiac, left gastric and cranial mesenteric artery before joining the right aorta caudal to the heart. Like all reptiles, venous drainage from the pelvic limb drains into the kidney to form the renal portal system.

Venepuncture sites

(Murray 2000; Redrobe & MacDonald 1999)

- Jugular vein – This lies very superficially on the lateral side of the neck and runs from the tympanic membrane at the angle of the jaw to the base of the neck (Fig. 3.17).
- Dorsal coccygeal vein – The coccygeal vertebrae lack dorsal spines and the vein runs quite superficially.

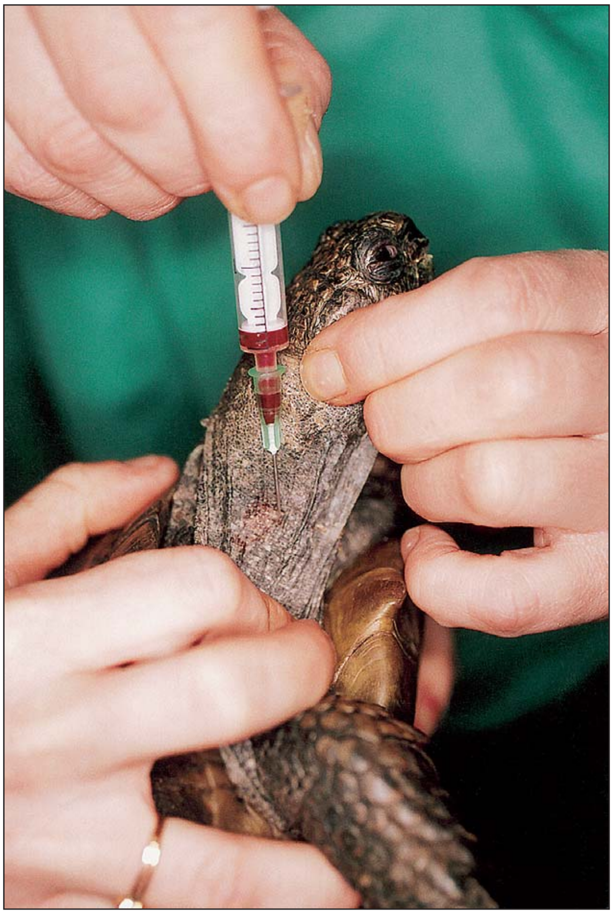


Figure 3.17 • Blood sampling from jugular vein in a Spur-thigh tortoise (*Testudo graeca*).

- Dorsal occipital venous plexus – This sinus cannot be visualized. The head is extended and needle inserted lateral to the cervical vertebrae, just cranial to the carapace. It is the best location in marine turtles.
- Toenail – This is least recommended as it is painful and samples can be contaminated with urates.

IMMUNE SYSTEM

The lymphatic circulation is intimately associated with the circulatory system in chelonia and can pose a major complication in blood sampling. The deep jugular trunk passes close to the jugular vein and a subpubic sinus, which drains the tail, cloaca, and caudal limbs can affect blood samples from the dorsal coccygeal vein.

The skin has a network of lymphatic vessels that are widely meshed, becoming superficial near the attachment of skin to the shell. The orbits have two lymphatic sinuses that extend into both eyelids. A single pair of lymphatic hearts lies at the most caudal part of the trunk, deep to the last vertebral shield of the carapace.

Some species, like the Red-eared sliders (*Trachemys scripta*) and European pond turtle (*Emys orbicularis*), have a lymphatic ring around the base of the neck (Ottaviani & Tazzi 1977) (Fig. 3.18).

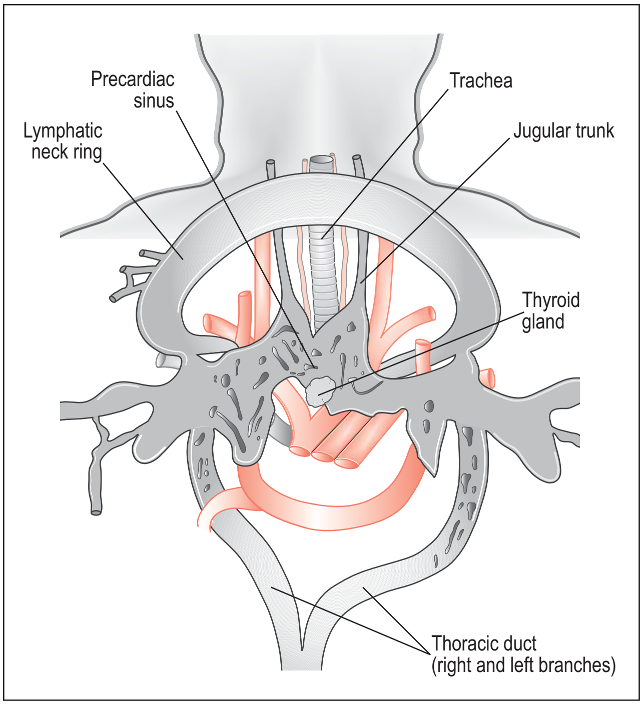


Figure 3.18 • Lymphatic neck ring in the Red-eared slider (*Trachemys scripta*) and European pond turtle (*Emys orbicularis*).

RESPIRATORY SYSTEM

Chelonia can make difficult anesthetic patients because they can easily switch to the dive reflex and employ anaerobic respiration (Fig. 3.19). They have the highest bicarbonate (HCO_3) level of all vertebrates, which helps them buffer lactic acid accumulation during anaerobiasis.

Figure 3.19 • Induction of anesthesia can be difficult in aquatic species.

Upper respiratory tract

Chelonia breathe with their mouth closed. Air enters via the external nares into the nasal cavity and passes through the partial hard palate to the pharynx. The glottis is easily visible at the back of the short, fleshy tongue. The trachea has complete cartilaginous rings. In Cryptodira species the trachea is very short and bifurcates rapidly to allow for head retraction.

Lower respiratory tract

The lungs are spongy and occupy a large volume in the dorsal half of the body cavity, although their volume is reduced to one fifth when the head and limbs are retracted (Gans & Hughes 1967). They are attached dorsally to the periosteum of the carapace and tightly against the pectoral and pelvic limb girdles. They are not surrounded by a pleural cavity and are only separated from the ventral cavity and viscera by a thin non-muscular postpulmonary septum, which plays no active part in respiration (Murray 1996b; Perry 1989).

Internally, chelonian lungs are surprisingly advanced for such a primitive reptile (Fig. 3.20). They are multicameral, as in the Monitor lizard, with a single intrapulmonary bronchus radiating into a network of bronchioles and highly vascular faveoli (Perry 1989). However, unlike in the Monitor lizard, the lungs are confined only to the dorsal half of the body, with the heart lying cranially near the pectoral inlet (Figs. 3.21–3.23) (see Chapter 4).

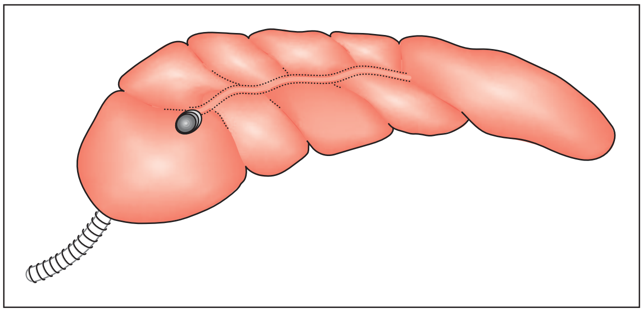


Figure 3.20 • Schematic drawing of multicameral lungs of Chelonia. Despite their ancient lineage and primitive appearance chelonians have more advanced lungs than snakes and some lizards.

CLINICAL NOTE

Remember, most chelonians have a very short trachea, so when intubating do not insert the endotracheal tube too far as you may be intubating one primary bronchus instead (Murray 1996a; Gans & Hughes 1967).

Ventilation

The absence of a diaphragm and the fact that they have modified their ribs, sternum, and vertebrae into a hard shell means there is no expandable chest (McCutcheon). Therefore, in order to breathe, chelonians have developed strong trunk muscles, which expand and contract the lungs with active inspiration and expiration (Fig. 3.24) (Gans & Hughes 1967; McCutcheon 1943; Pough 1998a). It is the action of these antagonistic muscles moving the ventral postpulmonary septum that draws air in and out of the lungs. Terrestrial species breathe regularly but aquatic species can only breathe when they surface for air, otherwise the high volume of air would act as a natural buoyancy aid.

CLINICAL NOTE

When Chelonia have their head retracted inside their shell they can no longer move their pectoral girdle, so they have to breathhold.

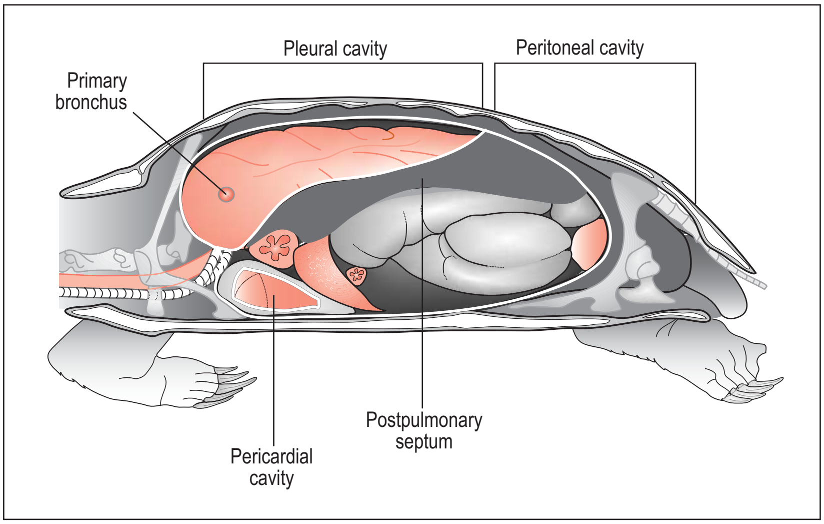


Figure 3.21 • Lateral view of chelonian (left lung, liver and stomach removed). The heart occupies a cranial position because the lungs are restricted to the dorsal thorax.

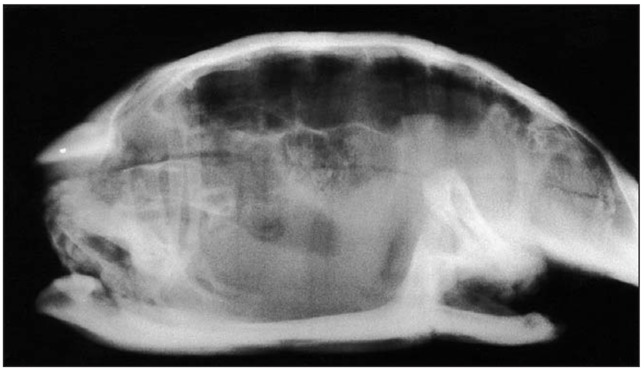


Figure 3.22 • Lateral radiograph (horizontal beam) showing lung fields.

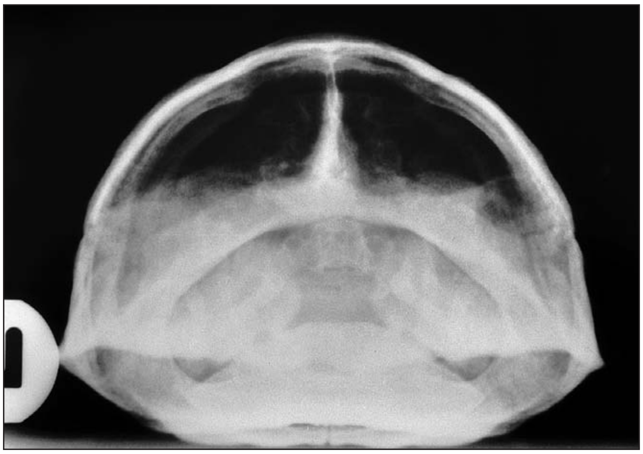


Figure 3.23 • Radiograph (horizontal beam) showing rostrocaudal view of lungs – the best view for assessing the lungs for pneumonia.

Terrestrial (tortoises)

The four groups of abdominal muscles vary between terrestrial and aquatic species.

Inspiration

The serratus muscle arises from the front of the carapace to insert on the coracoid while the abdominal obliquus inserts on the skin of the hindlimb. When these two muscles contract they create negative pressure and active inspiration. The forelimbs rotate out of the shell, pulling the septum ventrally and causing the lungs to expand and draw in air via the trachea and bronchi (Gans & Hughes 1967; Pough 2002; Wood & Lenfant 1976).

Expiration

The pectoralis muscle extends from the plastron to the humerus, and the tranversus abdominus originates from the back of the carapace. When these two muscles contract, the forelimbs rotate back into the shell, pulling the membrane forward and putting pressure on ventral viscera to expel gas (Gans & Hughes 1967; Pough et al. 2002).

Aquatic turtles

In aquatic species, respiration is aided by the hydrostatic pressure of water, which can draw air in and out of the lungs (Pough 2002). There are four groups of muscles involved in the respiratory cycle. Inspiration is created by the testocoracoideus, which runs from the carapace to the medial scapula and dorsal coracoid, and the obliquus abdominis muscles, which help expand the cavity to create negative pressure. Expiration is via the diaphragmaticus and the transversus abdominis muscle, which compresses the celomic cavity (McCutcheon 1943; Wood & Lenfant 1976).

CLINICAL NOTE

Chelonians cannot cough effectively as they lack a diaphragm. This factor combined with their huge lung volume and lack of a bronchi-ciliary transport system means they easily get pneumonia.

Accessory respiratory organs

Some semi-aquatic freshwater turtles possess the ability to absorb oxygen via well vascularized cloacal bursae, which they can use during periods of hibernation underwater. Others, like the softshelled turtles can remain submerged for hours in the mud, utilizing oxygen in the water by breathing through the skin and pharyngeal mucosa.

DIGESTIVE SYSTEM

About 25% of Chelonia are herbivorous (King 1996) and there are also many omnivores eating some plant matter in their diet. Omnivores tend to favor sedentary prey like molluscs and worms.

Chelonians have no teeth so are unable to chew. Instead, like birds, they have a short horny beak with sharp edges. Most herbivorous species have a row of hard chewing ridges on the palate to allow more precise biting of food. Snapping turtles have very sharp cutting edges to the jaws and can give quite a ferocious bite (King 1996).

The tongue is short and fleshy and the salivary glands produce mucus but no digestive enzymes. The esophagus leads to a simple, spindle-shaped and thicker walled stomach, which lies embedded in the left lobe of the liver. The liver is large and divided into two lobes, and a gall bladder may be found in the right lobe (Figs 3.25 and 3.26). In herbivores the large intestines are wide in circumference and are the site for microbial digestion. A cecum may be present but even in herbivores is not well developed. Digestive enzymes are produced by the stomach, small intestine, pancreas, liver, and gall bladder. Passage of food is slow and can take up to two to four weeks, allowing maximal nutrition to be absorbed (King 1996).

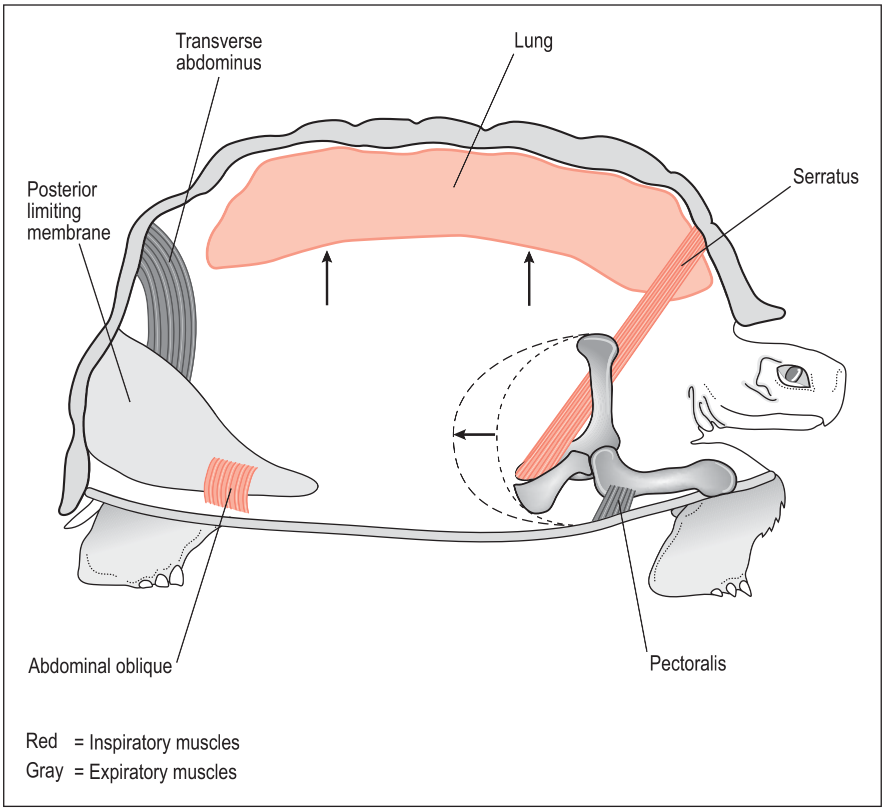

Transverse abdominus
Lung
Posterior limiting membrane
Serratus
Abdominal oblique
Pectoralis
Red = Inspiratory muscles
Gray = Expiratory muscles

Figure 3.24 • Lateral view of tortoise showing lungs and demonstrating inspiratory and expiratory muscles of respiration.
Red = Inspiratory muscles
Gray = Expiratory muscles

URINARY SYSTEM

Kidneys

The kidneys are large, flat, lobulated organs lying under the caudal carapace, just caudal to the acetabulum (Fig. 3.26). Unlike those in other reptiles, they lie symmetrically. Short ureters and genital ducts enter into a urogenital sinus, which opens into the floor of the cloaca. Urine passes from the urodeum retrograde into a large, saclike, ventrally placed urinary bladder. This is usually bilobed with the liver lying over the right lobe.

Terrestrial species use this to store water for long periods to facilitate water resorption. Some species have cloacal bladders, which may be extra water storage chambers and may also serve as respiratory chambers for species that hibernate underwater for weeks (Bentley 1976; Fox 1977).

CLINICAL NOTE

The proximity of the genital ducts to the bladder means eggs may drop into the bladder if the female strains while laying.

REPRODUCTIVE SYSTEM

SEXUAL DETERMINATION

- The male plastron is concave while the female's is flat or convex. This is more pronounced in species with high domed shells, to facilitate copulation (Zangerl 1970).
- The tail is often longer and thicker in the male.
- The vent in the male is situated beyond the outer margin of the carapace.
- Male aquatic species have longer claws on the forelimbs (Evans 1986).

Sex determination

Temperature-dependent sex determination is common in Chelonia and discussed in more detail in Chapter 2.

Male

The testes are long, yellow and oval and attached to the cranioventral pole of the kidneys. The vasa deferentia run alongside the ureters to the cloaca. The ventral proctodeum is modified and thickened into a single phallus (Fig. 2.13).

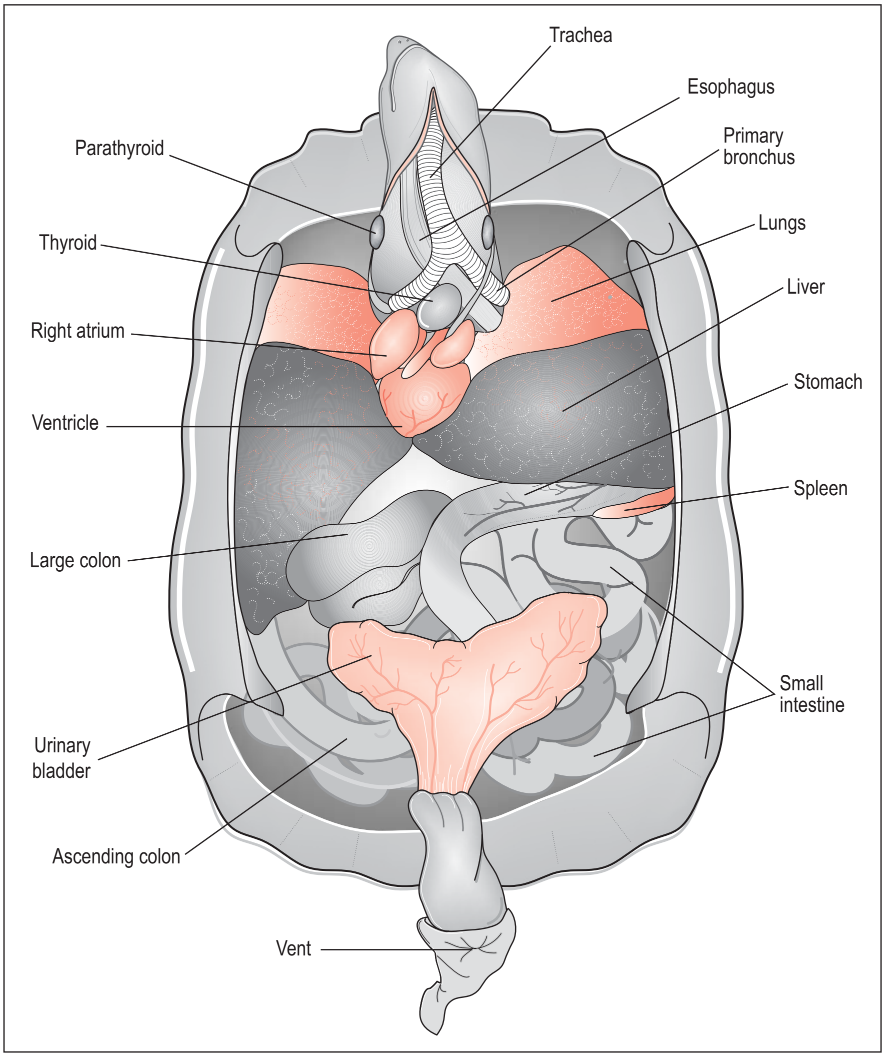


Figure 3.25 • Ventral view of chelonian after plastron and trunk muscles have been removed to show gross anatomy.

This consists of two pairs of fibrous tissue separated by a central trough that, unlike in snakes and lizards, cannot be inverted. This tissue is highly vascular and when inserted into the cloaca of the female it becomes engorged. Semen is conveyed down the central sulcus. A retractor muscle then returns the phallus back into the cloaca (Bellairs 1969c).

Female

The paired ovaries lie symmetrically, cranial to the kidneys. They are irregular, saclike, and paired, with different sized ova that become prominent with mature follicles (Fig. 3.27). The females in some species can retain sperm in their uterus so they can successfully fertilize two or more clutches, often several years after copulation (Pough 1998a).

All chelonians are oviparous. Temperate species lay eggs with soft, flexible leathery shells that can absorb or lose moisture. Tropical species and most land tortoises lay an egg with a hard brittle shell to prevent water loss. In general soft-shelled eggs develop more rapidly than hard-shelled ones. Incubation can be as little as 2 months in some temperate species but 8–9 months in some tropical species. Egg hatching will depend on climate conditions like spring warmth or seasonal rains (Minnich 1982; Pough 1998b).

Copulation

Courtship and mating is very vocal with lots of grunting, crying, and barking. The male mounts from the rear and fertilization is internal.

GENERAL INTEREST

The male Red-eared slider swims backward in front of the female, stroking her face with his long claws and eventually luring her underwater for copulation. As it can take over an hour they have to occasionally surface for air!

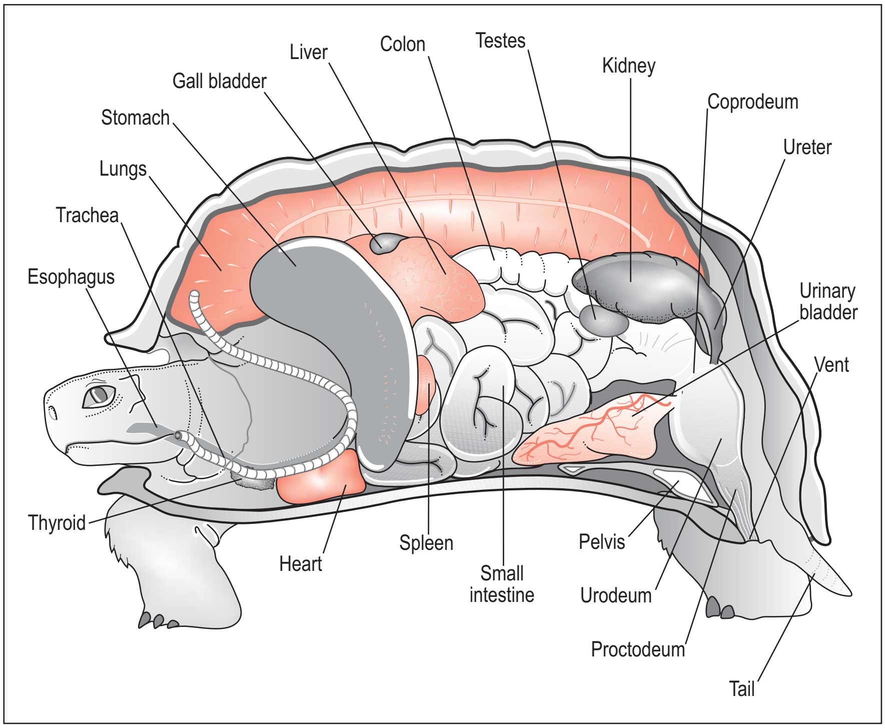


Figure 3.26 • Midsagittal view of chelonian to show gross anatomy.

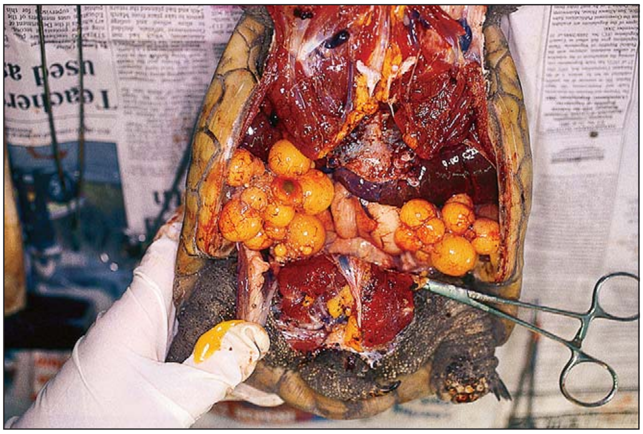


Figure 3.27 • Post mortem appearance of ovarian follicular stasis in a solitary kept Spur-thigh tortoise (*Testudo graeca*) that died from pneumonia. Note the huge muscles mass of the cranial and caudal trunk muscles.

SENSES

Sight

Vision is highly developed and based on color vision. The orbit is walled on three sides and, as in lizards and birds, the globe is surrounded by scleral ossicles. They have scaled eyelids and a third eyelid is usually present. The lacrimal gland is modified into a salt gland in marine turtles. They have no nasolacrimal ducts and so lose tears by evaporation (Underwood 1970).

Accommodation occurs by contraction of both the ciliary muscles and the iris sphincter muscle, which is presumably an adaptation to terrestrial and aquatic existence. Chelonians also have an upwardly tilted palpebral aperture to aid swimming with the head on the surface of the water (Underwood 1970). The retina is avascular.

GENERAL INTEREST

Female sea turtles have often been described as weeping as they dig their nest and lay their eggs. This is not for sentimental reasons but simply due to tear overflow from the salt gland that occurs because of the absence of a lacrimal duct.

Olfaction

The sense of smell is well developed and linked both to the nasal cavity and Jacobson's organ. In chelonians, however, this organ is not a distinct outpouching but just a localized area of sensory epithelium (Parsons 1970).

Hearing

Hearing is poor. There is no external ear but an inconspicuous tympanic membrane covered in skin is present in some species. The columella and tympanic cavity are large and a common site for aural abscesses. The middle ear communicates with the pharynx through the narrow auditory (eustachian) tube which is visible inside the pharynx just caudal to the jaw (Murray 1996a; Young 1997).

CLINICAL NOTE

Chelonia with a diet deficient in Vitamin A develop squamous metaplasia of the tympanic cavity lining. This allows bacteria ascending the eustachian tube from the pharynx to colonize, leading to chronic aural abscessation. Unlike in mammals, this pus is caseous and solid because reptiles lack the lysozymes to produce liquid pus; hence surgery is necessary to debride and curette the lesion, along with a requirement to improve husbandry and diet (Murray 1996a).

KEY POINTS

- Lymphatics lie very close to blood vessels so lymphdilution is common
- Trachea is short and lungs have large volume
- Dive reflex and easy anaerobic metabolism can complicate anesthesia
- Bladder is large
- Temperature sensitive determination is common
- Vision and smell are advanced but hearing is poor

REFERENCES

Bartholomew, G. A. (1982) Physiological control of body temperature. In C. Gans & F. H. Pough (eds.), *Biology of the reptilia*. Vol. 12, Physiology C. London: Academic Press. pp. 167–204.

Bellairs, A. (1969a) *The life of reptiles*. Vol. 1. London: Weidenfeld and Nicolson. Body form, skeleton and locomotion; pp. 44–116.

Bellairs, A. (1969b) *The life of reptiles*. Vol. 2. London: Weidenfeld and Nicolson. The skin; pp. 283–332.

Bellairs, A. (1969c) *The life of reptiles*. Vol. 2. London: Weidenfeld and Nicolson. Sex and reproduction; pp. 390–433.

Bellairs, A. (1969d) *The life of reptiles*. Vol 2. London: Weidenfeld and Nicolson. Growth, age and regeneration; pp. 458–488.

Bentley, P. J. (1976) Osmoregulation. In C. Gans & W. R. Dawson (eds.), *Biology of the reptilia*. Vol. 5, Physiology A. London: Academic Press. pp. 356–408.

Boyer, T. H., & Boyer, D. M. (1996) Turtles, tortoises and terrapins. In D. R. Mader (ed.), *Reptile medicine and surgery*. Philadelphia: WB Saunders. pp.61–78.

Enlow, D. H. (1970) The bone of reptiles. In C. Gans (ed.), *Biology of the reptilia*. Vol. 1, Morphology A. London: Academic Press. pp. 45–77.

Evans, H. E. (1986) Reptiles – Introduction and anatomy. In M. E. Fowler (ed.), *Zoo and wild animal medicine*, 2nd edn. Philadelphia: WB Saunders. pp. 108–132.

Fox, H. (1977) The urogenital system of reptiles. In C. Gans & T. Parsons (eds.), *Biology of the reptilia*. Vol. 6, Morphology E. London: Academic Press. pp. 1–122.

Gans, C. & Hughes, G. M. (1967) The mechanism of lung ventilation in the tortoise *Testudo Graeca Linne*. *Journal of Experimental Biology 47*, 1–20.

Gregory, P. T. (1982) Reptilian hibernation. In C. Gans (ed.), *Biology of the reptilia*. Vol. 13, Physiology D. London: Academic Press. pp. 53–140.

Hoffstetter, R., & Gasc, J. P. (1970) Vertebrae and ribs of modern reptiles. In C. Gans (ed.), *Biology of the reptilia*. Vol. 1, Morphology A. London: Academic Press. pp. 201–302.

King, G. (1996) *Reptiles and herbivory*. London: Chapman & Hall. Turtles and tortoises; pp. 47–60.

McCutcheon, F. H. (1943) The respiratory mechanism of turtles. *Physiological Zoology 16*: 255.

Minnich, J. E. (1982) The use of water. In C. Gans & F. H. Pough (eds.), *Biology of the reptilia*. Vol. 12, Physiology C. London: Academic Press. pp. 325–386.

Murray, M. J. (1996a) Aural abscess. In D. R. Mader (ed.), *Reptile medicine and surgery*. Philadelphia: WB Saunders. pp. 349–352.

Murray, M. J. (1996b) Pneumonia and normal respiratory function. In D. R. Mader (ed.), *Reptile medicine and surgery*. Philadelphia: WB Saunders. pp. 396–405.

Murray, M. J. (2000) Reptilian blood sampling and artifact considerations. In A. Fudge (ed.), *Laboratory medicine – avian and exotic pets*. Philadelphia: WB Saunders. pp. 185–191.

Ottaviani, G., & Tazzi, A. (1977) The lymphatic system. In C. Gans & T. Parsons (eds.), *Biology of the reptilia*. Vol. 6, Morphology E. London: Academic Press. pp. 315–458.

Parsons, T. S. (1970) The nose and Jacobson's organs. In C. Gans (ed.), *Biology of the reptilia*. Vol. 2, Morphology B. London: Academic Press. pp. 99–185.

Perry, S. F. (1989) Structure and function of the reptilian respiratory system. In S. C. Wood (ed.), *Comparative pulmonary physiology – current concepts*. New York: Dekker. pp. 193–237.

Pough, F. H., Andrew, R. M., Cadle, J. E. et al. (1998a) *Herpetology*. Englewood Cliffs, N.J: Prentice Hall. Classification and diversity of extant reptiles; pp. 75–133.

Pough, F. H., Andrew, R. M., Cadle, J. E. et al. (1998b) *Herpetology*. Englewood Cliffs, N.J: Prentice Hall. Reproduction and life history; pp. 204–235.

Pough, F. H., Janis, C. M., & Heiser, J. B. (2002) *Vertebrate life*, 6th edn. Englewood Cliffs, N.J: Prentice Hall. Turtles; pp. 270–294.

Redrobe, S., MacDonald, J. (1999) Sample collection and clinical pathology of reptiles. In D. R. Reavill (ed.), *Clinical pathology and sample collection*. The Veterinary Clinics of North America: Exotic animal practice. Vol. 2. Philadelphia: WB Saunders. pp. 709–730.

Seymour, R. S. (1982) Physiological adaptations to aquatic life. In C. Gans (ed.), *Biology of the reptilia*. Vol. 13, Physiology D. London: Academic Press. pp. 1–41.

Underwood, G. (1970) The eye. In C. Gans (ed.), *Biology of the Reptilia*. Vol. 2, Morphology B. London: Academic Press. pp. 1–93.

Walker, W. F. (1973) The locomotor apparatus of testudines. In C. Gans & T. Parsons (eds.), *Biology of the reptilia*. Vol. 4, Morphology D. London: Academic Press. pp. 1–99.

Wood, S. C., & Lenfant, C. J. (1976) Respiration: Mechanics, control and gas exchange. In C. Gans & W. R. Dawson (eds.), *Biology of the reptilia*. Vol. 5, Physiology A. London: Academic Press. pp. 225–267.

Young, B. A. (1997) Hearing, taste, tactile reception and olfaction. In L. Ackermann (ed.), *The biology, husbandry and healthcare of reptiles*. Vol. 1, The Biology of reptiles. N.J.: TFH Publications. pp. 185–213.

Zangerl, R. (1970) The turtle shell. In C. Gans (ed.), *Biology of the Reptilia*. Vol. 1, Morphology A. London: Academic Press. pp. 311–337.

4

Lizards

INTRODUCTION

Lizards are the most widely distributed of all the reptiles and are found on every continent, although most species are found in tropical areas. They are the most diverse of all reptiles, varying from arboreal, flying, and rock dwellers to semiaquatic and to the Galapagos marine iguana (*Amblyrhynchus cristatus*), which feeds on algae.

In comparison to the shelled chelonians and elongate limbless snakes, lizards are the least highly specialized. Some lizard species, like the slow worm (*Anguis fragilis*), have lost their limbs so the main way to distinguish lizards from snakes is that they have a short trunk with a long tail, whereas snakes have the converse. They also tend to have four limbs, a shorter, flatter tongue, moveable eyelids, and external ear openings (Pough 1998a). The two halves of the lower jaw are firmly united in a mandibular symphysis and they have several rows of scales on their ventral abdomen (Table 4.1).

Longevity

Smaller lizards live for less than 5 years although Leopard geckos (*Eublepharis macularius*) have been reported to live for 28 years. Larger lizards like iguanas can live for 10 to 20 years. However, the record lies with a European slow worm (*Anguis fragilis*) which lived 54 years! (Bellairs 1998h).

Size

Lizards range in size from tiny geckos, weighing a few grams, to the Komodo dragon (*Varanus komodoensis*), which is 3.6 m long and can weigh up to 136 kg (Bellairs 1998h). Eighty percent of lizards, however, weigh under 20 g (Evans 1986; Pough 2002).

TAXONOMY

The order Squamata (*squama* is Latin for "scale") comprises 95% of reptiles species and is divided into three suborders. In fact, 51% of known reptiles belong to just three squamate families: the colubrid snakes (23%), skinks (15%) and geckos (13%) (Uetz 2000). The Amphisbaenia (worm lizards) are less well known as they are underground burrowing lizards and are outside the scope of this book. The remaining suborders are the more familiar Serpentes (snakes) and Sauria/Lacertilia (lizards). Lizards and snakes have extremely flexible

Table 4.1 Morphological differences between lizards and snakes

	Sauria (lizards)	**Serpentes (snakes)**
Limbs	Absent, two, four	Absent (vestigial)
Tongue	Short	Elongate
Eyelids	Present in most species	Absent
External ear	Present	Absent
Trunk	Short	Long
Tail	Long	Short
Mandibular symphysis	Present	Absent
Ventral scales	Several rows	Single scales (Gastropeges)

Table 4.2 Common Saurian infraorders and families

Infraorder	**Family**	**Common species**
Iguania	Iguanidae	Iguana, Anole, Chuckwallas, Basilisk
	Agamidae	Agamas, Water & Bearded dragons
	Chamaeleonidae	Chameleons
Gekkota	Gekkonidae	Geckos
Scincomorpha	Teiidae Scincidae	Tegus, Ameivas Skinks
Varanoidea	Helodermatidae Varanidae	Beaded lizards, Gila monster Monitors, Goanna, Komodo dragon

skulls, known as kinetic skulls, whereas worm lizards have a heavily ossified skull which acts like a battering ram while burrowing.

GENERAL INTEREST

Worm lizards are mainly limbless, subterranean lizards and can move forward and backward with ease underground (amphisbaenia means "one who goes in both ways" in Greek). Their eardrums and eyes are covered with opaque skin. Unlike lizards, they have very short tails and their skulls are heavily ossified to facilitate digging (Pough 2002).

THERMOREGULATION

The maximum temperature at which a lizard can survive varies with the natural habitat of the species. Temperate lizards die when the temperature exceeds 30º C, tropical ones at above 35º C, and desert lizards cannot exist in temperatures above 46º C. Tropical species can estivate at times of drought; temperate and subtropical species can hibernate.

Heliothermic shuttling

Using the hypothalamus as a thermostat (and the parietal eye in some species), lizards alter their behavior to regulate their body temperature. In the early morning, lizards choose to bask on vegetation rather than on rocks that have cooled during the night and that would absorb heat from them. Later they move to the more solid surfaces, which have heated up by then. If they get too hot they seek shade and, as sunset approaches, they seek shelter before the cold night (Pough 1998c).

Color change

Many lizards are dark colored in the morning, which enables them to absorb heat and lighten in color as the body warms up. Some desert lizards have scales with different infrared absorption dorsally and ventrally so they can absorb or emit heat depending on the time of day (Bellairs 1969d).

Body posture

Desert lizards can stretch their limbs and lift their bodies high above the warm surface. Others use the heat of solid objects warmed by the sun; for example, geckos may rest under the bark of trees.

GENERAL EXTERNAL ANATOMY

In general lizards are elongated and circular in cross-section, but arboreal chameleons are vertically compressed and some lizards, like the Bearded dragon (*Pogona vitticeps*), are horizontally compressed (Fig. 4.1).

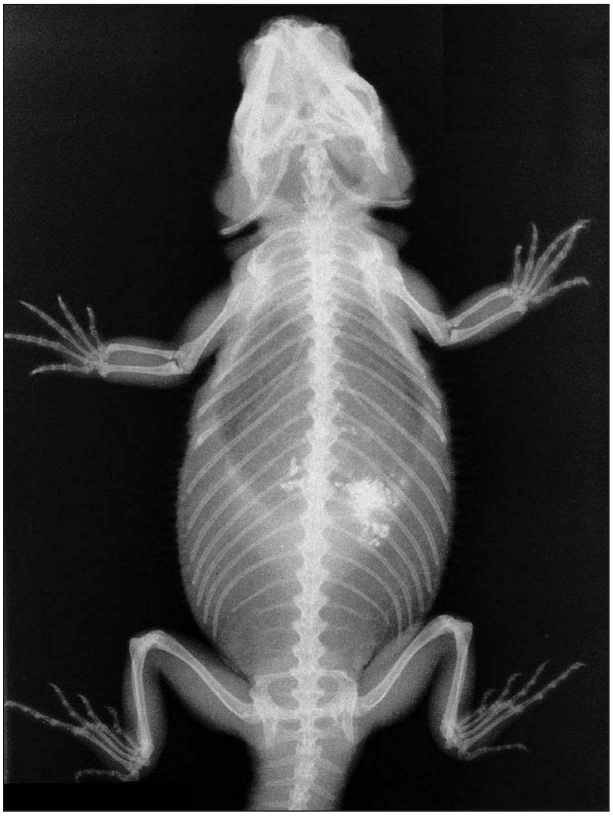


Figure 4.1 • Dorsoventral radiograph of normal Bearded dragon (*Pogona vitticeps*). Some substrate is visible in the stomach.

Family: Iguanidae

These are moderate to large in size and include many herbivorous species. They have a large, laterally compressed body with nuchal and dorsal crest, large gular pouch, and conspicuous subtympanic plate. The tail is up to three times the snout-to-vent length and can be whip like. Femoral pores are prominent in the male. Males are generally more brightly colored, some displaying an orange hue in the mating season. The coloring of females tends to wash out with age. Iguanas are pleurodont and have nasal salt glands. Several species have a prominent parietal eye. Nearly all are oviparous. Many have partitions in the colon to slow down food ingesta (Evans 1986; Pough 1998b).

Examples:

Green iguana (*Iguana iguana*) (Fig. 4.2), Marine iguana (*Amblyrhynchus cristatus*), Chuckwalla (*Sauromalus* spp.), Basilisk (*Basilicus* spp.).

Family: Agamidae

These are mainly terrestrial lizards with well-developed limbs and are the old world equivalent of Iguanidae. They have acrodont teeth and some species have almost rodent-like incisors at the front of the jaw. Some species have sexually dimorphic crests and spines. They are mainly oviparous.

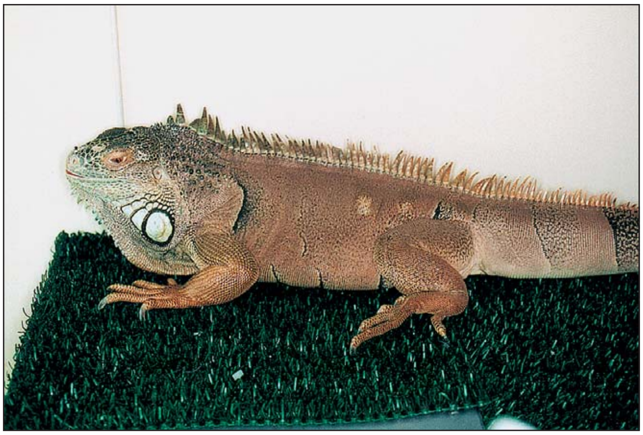


Figure 4.2 • Green iguana (*Iguana iguana*).

The South-east Asian Flying lizard (*Draco volans*) is the only lizard capable of gliding flight. This is achieved by having elongated ribs supporting webs of skin which can be opened like a fan for gliding. The Australian Frilled lizard has a frill which it can erect when danger threatens (Pough 1998b).

Examples:

Flying lizard (*Draco volans*), Frilled lizard (*Chlamydosaurus kingii*), Water dragon (*Physignathus* sp.) (Fig. 4.3), Bearded dragon (*Pogona vitticeps*).

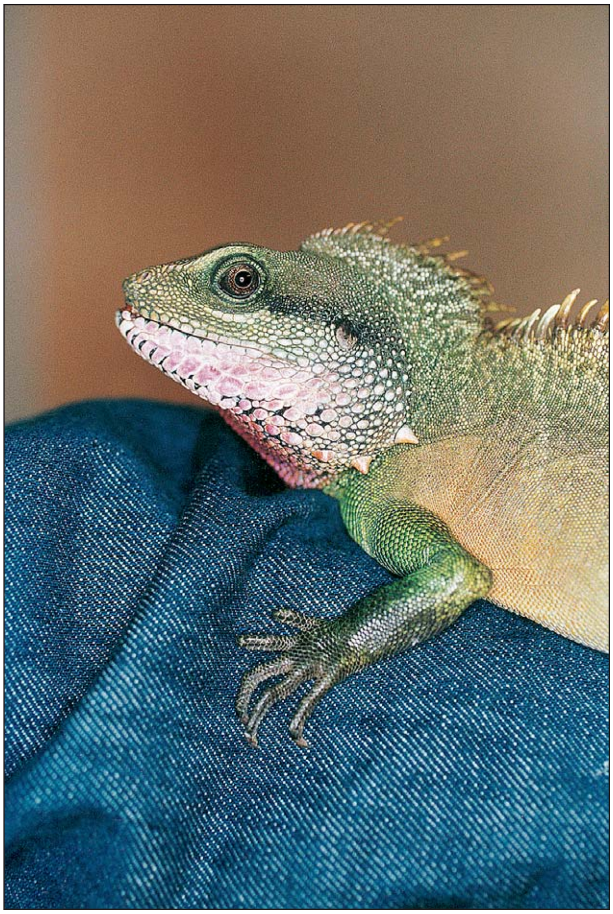


Figure 4.3 • Male Water dragon (*Physignathus cocincinus*).

Family: Chameleonidae

These are arboreal with a laterally compressed body and are mainly diurnal and insectivorous. The upper and lower eyelid is fused to form a pyramid mound with the eye as the aperture in the center. Each eye is capable of independent movement and they use accommodation to measure distance. The eye lens is like a telephoto lens and the large retina and high number of cones provide the chameleon with large visual images of its prey (Evans 1986).

The tongue is rapidly extensible to a distance of at least twice the animal's trunk length and is used for apprehending insect prey. The hyoglossal skeleton is modified into an extension called the *processus entoglossus*, which at rest keeps the tongue folded in pleats at the back of the mouth. A powerful accelerator muscle propels the tongue forward like a spring. The tongue tip is also sticky to catch the prey. Jacobson's organ is poorly developed.

Chameleons have very specialized skulls with their parietal crest raised into a casque. They have lost the skull kinesis seen in other lizards, which was presumably made redundant by the powerful tongue (Pough 1998e). The acrodont teeth, unlike in other species, do not have pleurodont teeth rostrally as the premaxilla is quite reduced with few teeth there at all. The chameleons' laterally compressed bodies and prehensile feet enable them to keep their center of gravity over a narrow support base. Their vertical limbs and highly mobile pectoral girdle gives them a longer step and the ability to reach forward more onto branches. The feet are zygodactyl, with toes fused together and opposed in groups of two and three (Fig. 4.12). The tail is prehensile and usually tightly coiled distally, with no autotomy. Rapid color changes are possible. Sexual dimorphism is common. They can be oviparous or viviparous (Bellairs 1969a, 1969f; Pough 1998b).

Examples:

Yemen veiled chameleon (*Chamaeleo calyptratus*) (Fig. 4.4), Parson's chameleon (*Calumma parsonii*).

Family: Gekkonidae/Eublepharidae

These are crepuscular or nocturnal insectivores with a flattened head and body. Most have adhesive toe pads which contain rows of tiny overlapping scales ventrally called *lamellae*. Each lamella has tiny, branching hairs called *setae* which can number up to one million in some gecko species. The ends of these setae are spatulate and it is the friction between these endings that creates the adhesive qualities of the feet and enables them to walk across ceilings and glass, even holding on by only one foot (Bellairs 1969a; Evans 1986; Pough 1998b).

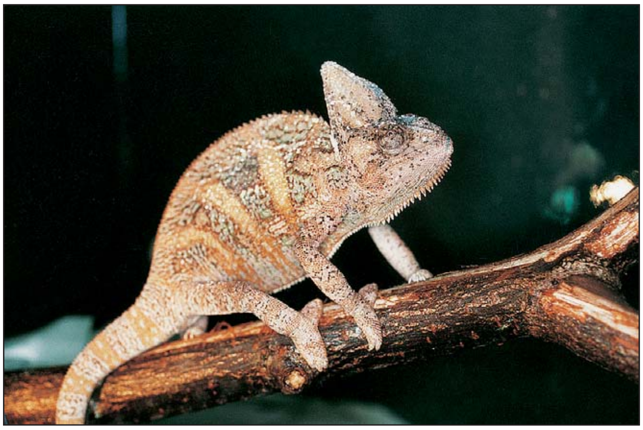


Figure 4.4 • Yemen veiled chameleon (*Chamaeleo calyptratus*) perching, showing high helmet casque and zygodactyl feet.

Many have loose skin and fat pads in the tail. Autotomy is common. Many lack eyelids which, like snakes, are fused to form a spectacle. They are not sexually dimorphic. They are oviparous and lay very hard-shelled eggs. Eublepharids are unusual in that they are terrestrial and have eyelids. They lack the adhesive lamellae and so are unable to climb.

Examples:

Leopard gecko (*Eublepharis macularius*), Tokay gecko (*Gekko gecko*), Standing's day gecko (*Phelsuma standingi)*.

Family: Varanidae

These are the giants of the lizard world and can reach a length of 3.6 m (Komodo dragon). Often called monitor lizards or, in Australia, "goannas." They are stocky with smooth scales. The tongue is forked for half its length and, as in snakes, is used more for exploration than tasting (Evans 1986). In some species ossification of the hemipenes can be seen on radiographs. Despite their size they are active predators with higher metabolic rates than most other lizards (Bennett, AF 1972). They are oviparous and have no autotomy (Pough 1998b).

Examples:

Komodo dragon (*Varanus komodoensis*), Bosc monitor (*Varanus exanthematicus*).

Family: Scincidae

These are a large terrestrial family that live mostly on or underground. They are small to medium in size (5–20 cm), are smooth scaled and are glossy in appearance. Osteoderms are present beneath the scales and the young often have blue tails (Pough 1998b). The limbs are short in relation to the body and some species are completely limbless. (Different species may have four limbs, two limbs or no limbs) (Fig. 4.5). They have a prominent ear opening; eyelids are fused to form a spectacle in some. The tail can be lost and regenerates. Some species are oviparous; some are viviparous with well-developed placentation. Except for the herbivorous arboreal Solomon Island skink they are mainly insectivorous (Evans 1986; Pough 1998b).

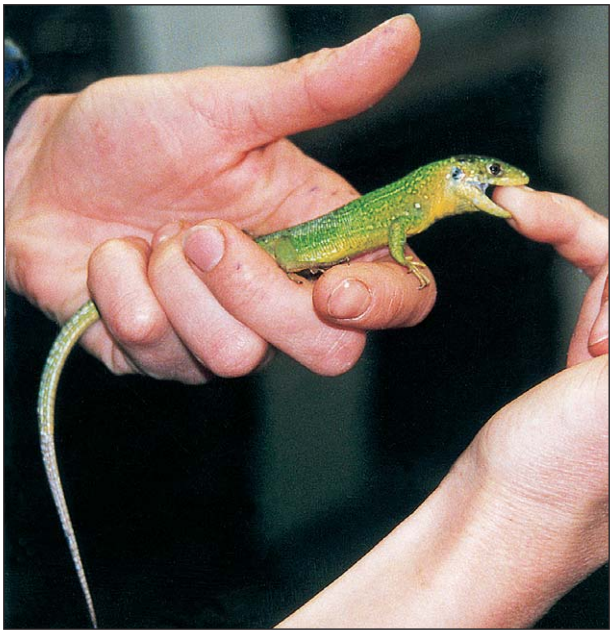


Figure 4.5 • Skinks have short limbs relative to body size and prominent ear openings. The tail can be lost and regenerates.

Examples:

Blue-tongued skinks (*Tiliqua* spp.), Solomon Island skink (*Corucia zebrata*).

SKELETAL SYSTEM

Skull

In most species (except burrowing lizards and skinks) the head is narrower than the body. Like snakes, lizards have a kinetic skull which is thought to enable the upper and lower jaw to be closed simultaneously over prey (Figs. 4.6 and 4.7). The lower jaw is further increased in gape by a condition known as *streptostyly*. This is when the quadrate bone has no firm connection (owing to the absence of the temporal arch) and can move backward and forward. The main advantage of this is that it gives the adductor muscles that close the jaw a better mechanical advantage when biting (Bellairs 1969a; King 1996b).

Although lizards have a large gape a united mandibular symphysis means they cannot open their mouths as wide as snakes. They compensate by having stronger jaws to help them immobilize, crush or tear at prey.

The adductor muscles extend from the temporal region to the lower jaw (Fig. 4.8). The main adductor muscle is the pterygoideus, which arises from the pterygoid bones on the palate and inserts on the caudal aspect of the lower jaw where it forms a large belly of muscle. It is this muscle that

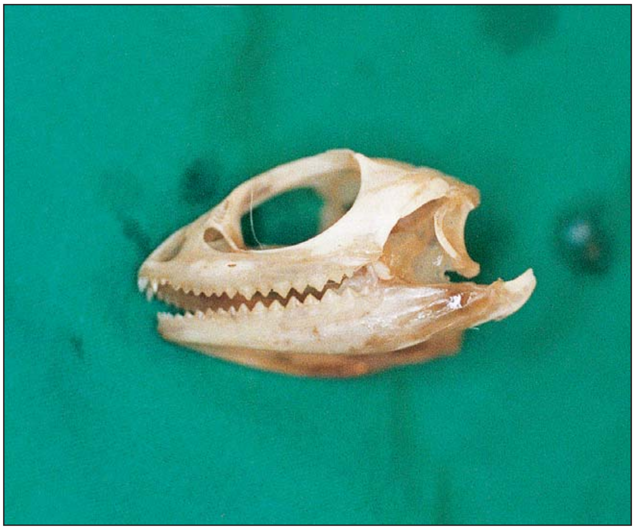


Figure 4.6 • Skull of juvenile bearded dragon (*Pogona vitticeps*).

can give the heavy jowled appearance to male lizards. The depressor mandible, which opens the jaw, arises from the back of the skull and inserts on the retroarticular process of the mandible. It is much weaker than the muscles that close the jaw (Bellairs 1969b; King 1996a).

CLINICAL NOTE

Always use a mouth gag when examining the mouths of large healthy lizards as the jaw can close like a trapdoor causing considerable damage and pain to unwary fingers.

Lizards are very mobile, having a flexible backbone, well-developed legs, and a long tail for counterbalance. All the vertebrae except the cervical ones bear ribs, leaving little flank area. Ventrally the ribs either join the sternum, the opposite member, or end free in the body wall. The number of tail vertebrae is usually higher than the number of presacral vertebrae.

More primitive lizards and tortoises have short limbs directed sideways, giving them their characteristic swinging gait. Advanced lizards have rotated these limbs towards the body so that the elbow faces caudally and the knee cranially. This form of limb orientation creates limbs that act as better shock absorbers.

Pectoral girdle and forelimbs

The pectoral girdle is composed of the scapula, coracoid bone and clavicle, and often an interclavicle. The forelimb has a short humerus and radius/ulna, with two rows of carpal bones. Both fore and hind feet are pentadactyl and the number of phalanges follows the formula 2,3,4,5,3 (from thumb to fifth digit), which gives rise to an asymmetrical foot (Fig. 4.9).

Pelvic girdle and hindlimbs

The pelvic girdle consists of a caudodorsally directed ilium, ischium and pubis and is firmly braced against the sacrum. The hindlimb is longer than the forelimb, owing to the elongated femur and phalanges. The tarsal bones have fused to form two bones called the astragalus-calcaneum, which articulates with the tibia and fibula. Flexion occurs between this joint and the rest of the foot. The hind foot has the first four metatarsal bones lying together while the fifth metatarsal lies separated with a backward-pointing hook. This allows the fifth digit to be opposed to the first, giving a better grip (Bellairs 1969a; King & Custance 1982; Pough 1998d) (Fig. 4.10).

Burrowing lizards have lost their limbs but, unlike snakes, they still retain their pectoral and pelvic girdle. Some lizards

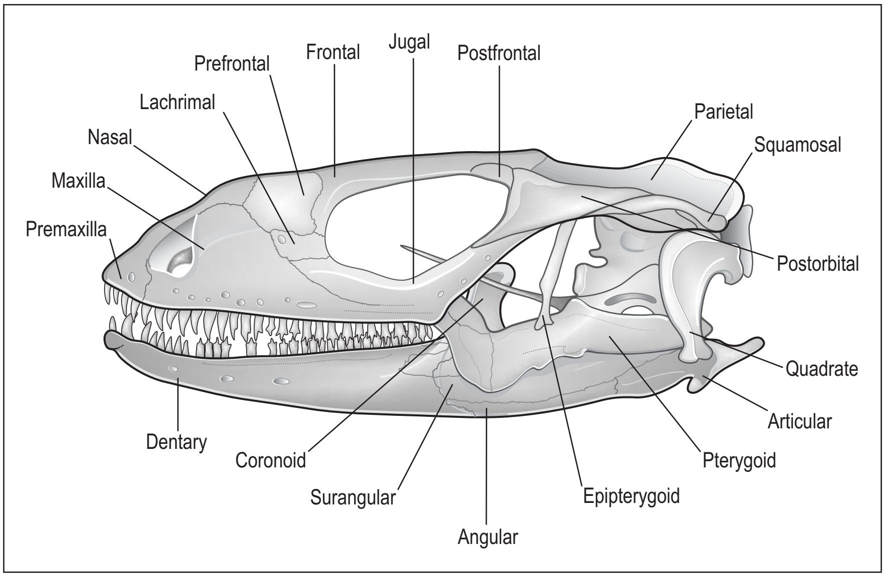


Figure 4.7 • Skull of lizard.

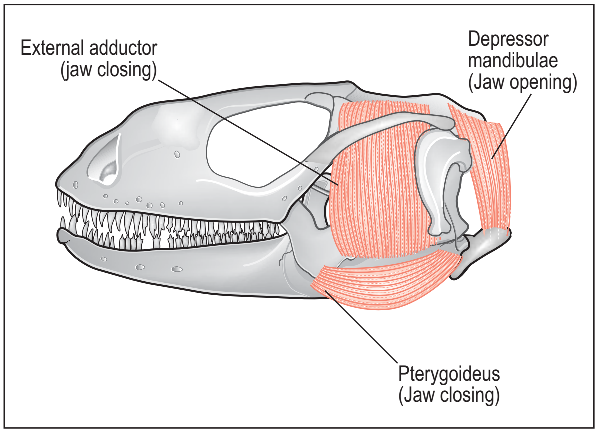


Figure 4.8 • Diagram of lizard skull showing main adductor (jaw closing) muscles. As the adductor muscles are extremely strong a mouth gag should be used when handling large lizards.

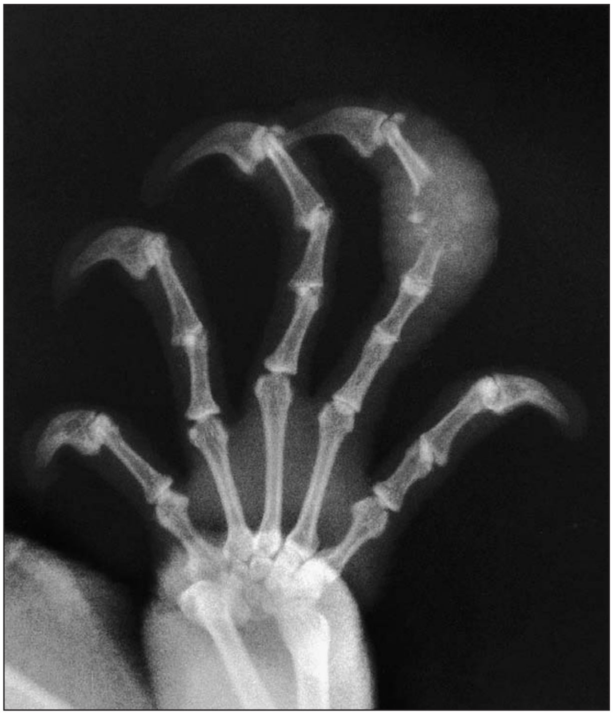


Figure 4.9 • Radiograph of right forefoot of Green iguana (*iguana iguana*) showing osteomyelitis at phalanges 3–4 of fourth digit. Both fore- and hind feet are pentadactyl in lizards with the number of phalanges following the formula 2,3,4,5,3 from thumb to fifth digit.

can hold their forelegs off the ground and run along on their hindlimbs in bipedal motion. Such species generally have a long tail as a counterbalance and lightweight thigh muscles.

Feet often have specialized adaptations. Many geckos have adhesive lamellae on their digits that allow them to walk on smooth vertical surfaces (Fig. 4.11). Chameleons have pincer-like zygodactyl feet with the first and second digits opposing the third and fifth (Figs. 4.4 and 4.12).

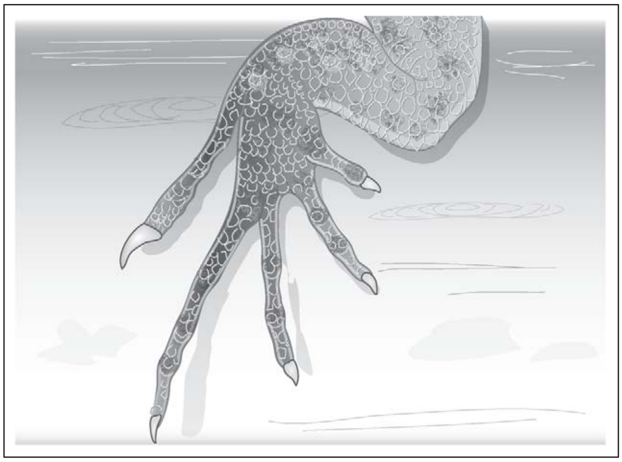


Figure 4.10 • Right hind foot of lizard showing first four metatarsals and separately attached fifth digit.

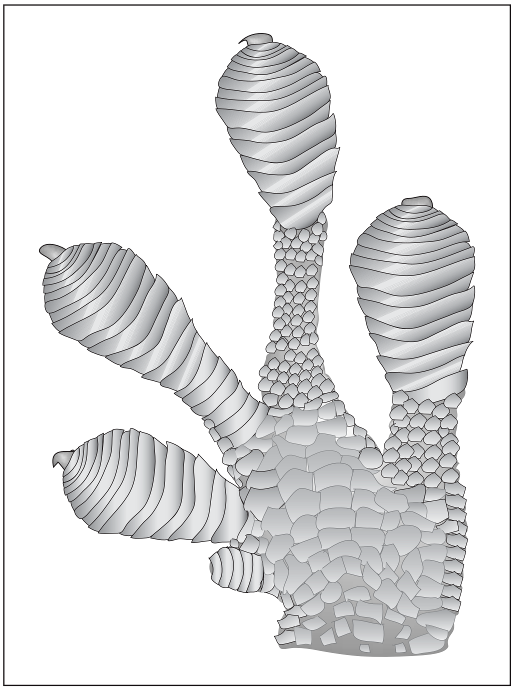


Figure 4.11 • Ventral view of gecko foot showing subdigital adhesive lamellae. These enable geckos to walk upside down on smooth surfaces.

GENERAL INTEREST

The Basilisk lizards (*Basilicus* spp.) have webbing on their feet and can run bipedally across water to escape from predators. This has earned them the local nickname of “Jesus Christ Lizard” (Bellairs 1969a; Pough 1998d).

Tail

Most reptiles have numerous caudal vertebrae and the tail can be prehensile, like in chameleons, or a site of fat storage, as in the Leopard gecko (*Eublepharis macularius*).

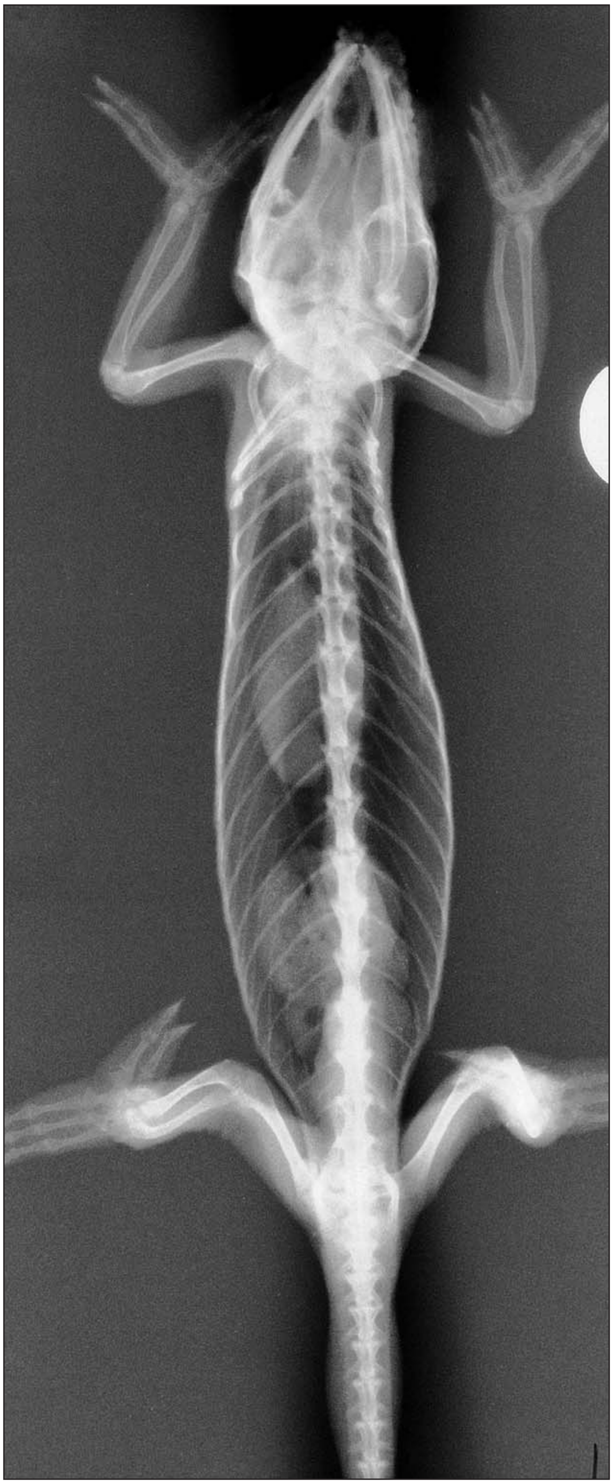


Figure 4.12 • Dorsoventral radiograph of Panther chameleon (*Furcifer pardalis*) showing zygodactyl feet.

Autotomy

Autotomy means "self-amputation" and is a mechanism to escape from predators. When the animal is attacked the brightly colored tail will break off and wriggle for a few minutes to distract the attacker, allowing the lizard to escape. It occurs in many lizards, such as the iguana, skink, and gecko species, where the tail is not essential for survival (Figs. 4.13 and 4.14). However, species like chameleons and monitors, which rely on their tail for climbing and defense, do not shed their tails. Similarly, the Marine iguana, which relies on its large rudder tail for swimming in the sea, lacks fracture planes.

Autotomy is created by a vertical fracture plane, containing no bone, passing through the body and part of the neural arch of each caudal vertebra (Bellairs 1998h; Bellairs & Bryant 1985; Evans 1986; Pough 1998b). This is a plate of cartilage or connective tissue that develops after ossification. These are not present in the cranial part of the tail so the cloaca and hemipenes are protected. In iguanas the fracture plane is replaced by bone during maturation, resulting in a more stable tail in adults.

CLINICAL NOTE

After autotomy the stump should never be stitched as the broken tail rapidly forms its own scab that is followed by growth of new epidermis within a week or two. Bleeding is minimal, owing to the action of sphincter muscles in the caudal arteries and valves in the veins. After about 2 weeks regeneration begins and a cylinder of cartilage is formed. This may become calcified, but as it has no individual tail vertebrae it is less flexible than the original model. It is innervated mainly by the last spinal nerves. It is finally covered by scales, which are often smaller and a different color from the original tail (Bellairs 1998h; Bellairs & Bryant 1985; Pough 2002).

KEY POINTS

- Kinetic jaw for wide gape
- Large well-developed adductor (jaw-closing) muscles, so mind your fingers!
- Hind foot has first four metatarsal bones lying together while fifth metatarsal lies separated with backward-pointing hook
- Tail can self amputate (autotomy)

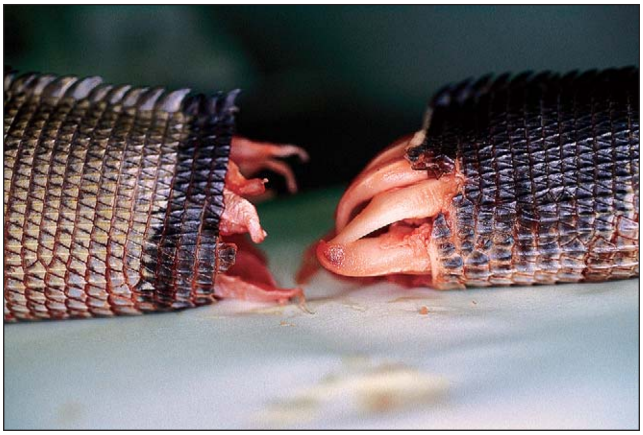


Figure 4.13 • Ends of tail post autotomy in a Green iguana (*iguana iguana*).

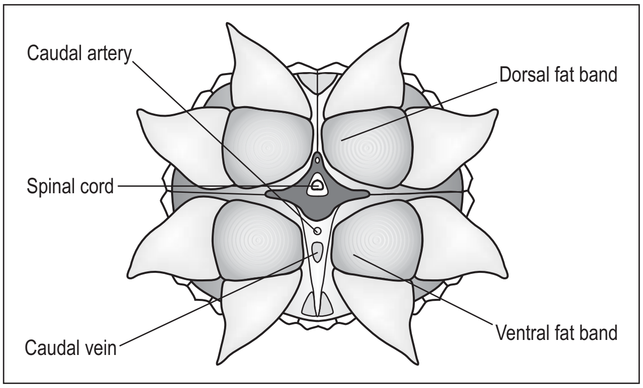


Figure 4.14 • Diagram of end on view of tail stump post autotomy.

CARDIOVASCULAR SYSTEM

The heart has three chambers: two atria and one ventricle, and lies cranially at the level of the pectoral girdle in most lizards (Fig. 4.15). In the more advanced lizards like monitors (*Varanus* spp.) the heart has descended caudally to lie in the middle of the thoracoabdominal cavity. Paired right and left aorta fuse caudal to it to form the dorsal aorta. A large ventral abdominal vein lies along the inner surface of the midline so this must be avoided when making a celiotomy incision (Barten 1996; Bennett & Mader 1996). A renal portal system is present, as in all reptiles.

Larger lizards (and crocodiles) have a vasovagal reflex whereby pressure on the eyeballs decreases the heart rate and blood pressure. This can be used by clinicians to perform non-painful procedures like radiography (Bennett, RA 1996).

CLINICAL NOTE

Incise paramedian or alternatively incise the linea alba with caution as the ventral abdominal vein is suspended in the broad ligament and is only a few millimeters away. Keep it protected with saline gauze during the procedure.

GENERAL INTEREST

The Horned lizard (*Phrynosoma cornutum*) is a desert ground dweller that is found in the southern USA and Mexico and which can squirt blood from its eye when under attack. This is achieved by a pair of muscles, which restrict the blood outflow from the internal jugulars, causing an increase in blood pressure and leakage from the ocular venous sinuses. When threatened the lizard closes its eyes, which become swollen, and then shoots out a fine stream of blood from the eyelid margins (Barten 1996; Evans 1986; White 1976).

Venepuncture sites

(See Murray 2000; Redrobe & MacDonald 1999.)

- Ventral coccygeal vein – The vein must be accessed caudal to the cloaca to avoid damaging the hemipenes in males. Access is usually about one third of the way from the vent and the needle is inserted ventrally in the midline. In some species a lateral approach may be used by inserting the needle perpendicular to the tail and ventral to the lateral vertebral processes (Murray 2000).
- Cardiac – as the heart cannot be held this is not as safe in lizards as in snakes.
- Axillary venous plexus – this is located near the shoulder joint at the caudal aspect of the humerus. Lymph dilution can occur.
- Ventral abdominal vein – this vein is very fragile so anesthesia is advisable to avoid lacerating it. The vein is approached two thirds of the distance caudally on the midline where it lies superficially just under the skin and muscle and is useful for lizards, like geckos, with short tails (Murray 2000).

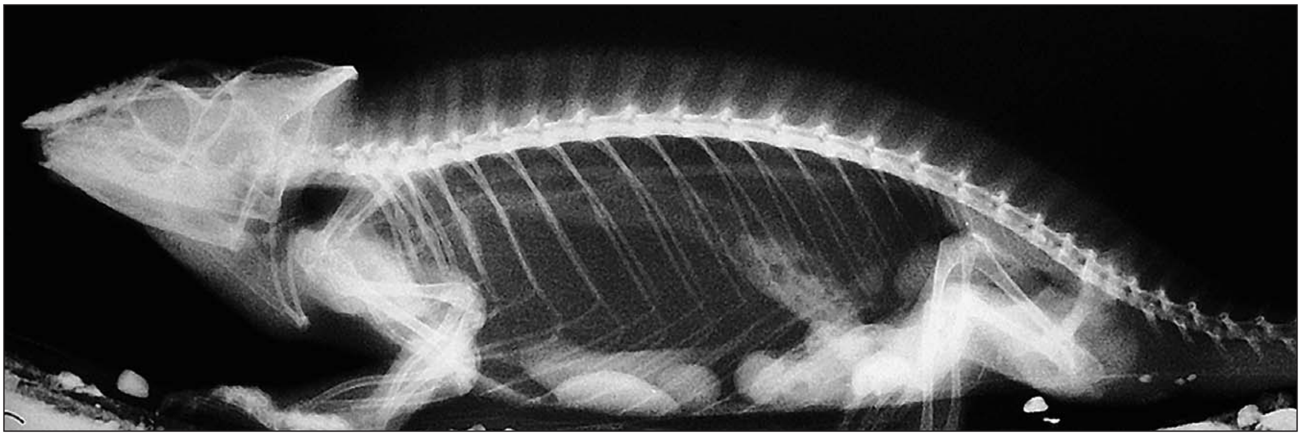


Figure 4.15 • Lateral (horizontal beam) radiograph of Panther chameleon (*Furcifer pardalis*). The heart lies at the pectoral inlet in most lizards. More advanced lizards like the monitors (*Varanus* spp.) have the heart lying more caudally in mid celom.

RESPIRATORY SYSTEM

Apart from gas exchange, the lizard uses its lungs for threat and display, buoyancy, escaping from predators and vocalization. It achieves this by having large volume, highly compliant lungs that can easily be inflated by gular pumping (Perry & Duncker 1978; Wood & Lenfant 1976).

Upper respiratory tract

The lizard palate has two long slit-like openings rostrally where the internal nares and Jacobson's organs open into the mouth and this can be a common site for discharges to develop. The glottis is variable in location and can be found very rostrally or at the back of the tongue, depending on the species. It is normally closed except during inspiration and expiration (Fig. 4.16).

Lower respiratory tract

The trachea has incomplete tracheal rings and bifurcates in the thoracic cavity near the heart. As they have no diaphragm, lizards breathe by expansion and contraction of the ribs. All three structural lung types are found in lizards: unicameral, paucicameral and multicameral (Fig. 4.17).

Unicameral lungs

Primitive lizards (e.g., the Green lizard, *Lacerta viridis*) lack any division between the pleural and peritoneal cavities. The heart lies in the pectoral inlet and the lungs form extensive hollow sacs that consist of a single chamber, hence "unicameral" (Fig. 4.18). They generally occupy the cranial part of the pleuroperitoneum but in some lizards like skinks (Scincidae) they have caudal non-respiratory dilatation, similar to airsacs. These airsacs are poorly vascularized and so can be a site of infection (Perry 1989; Perry & Duncker 1978).

Paucicameral lungs

Intermediate species have developed a membrane like a postpulmonary septum that connects to the pericardium. These paucicameral lungs have finer partitioning, with some having large caudal dilatations like airsacs (Fig. 4.19). In species like the chameleons these can be inflated to increase lung volume by over 40% in order to ward off predators (Perry 1989; Perry & Duncker 1978).

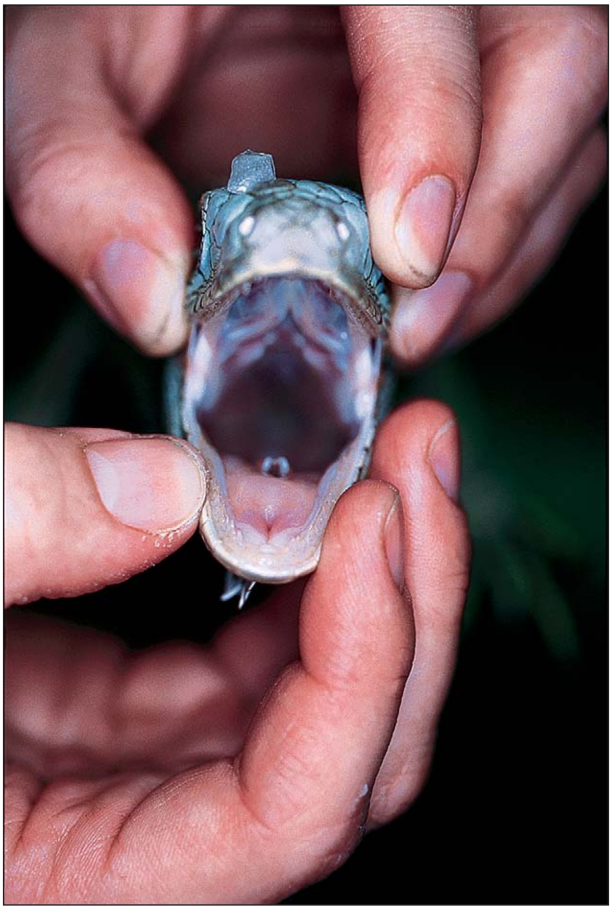


Figure 4.16 • Open mouth view of lizard showing open glottis. Respiration in reptiles is triphasic with the pause phase being the longest.

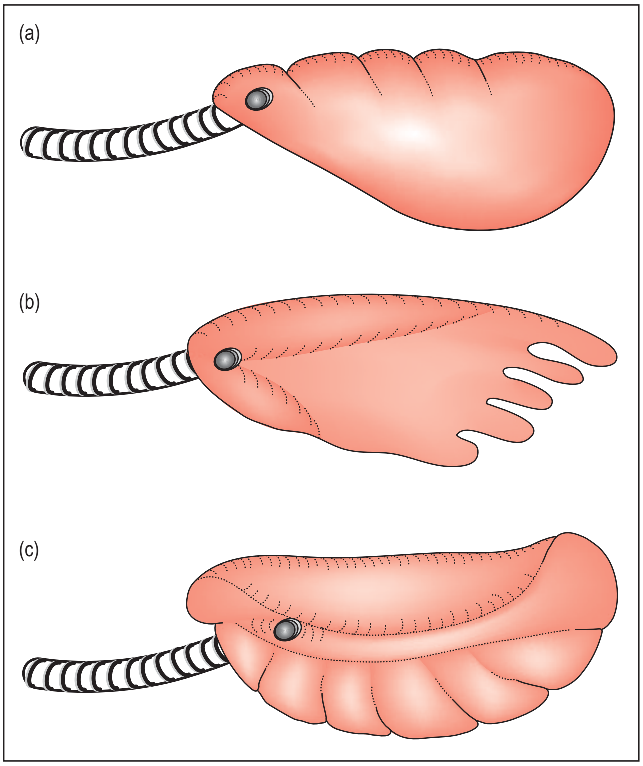


Figure 4.17 •
(a) Unicameral lung of simple lizard (e.g., Green lizard, *Lacerta viridis*)
(b) Paucicameral lungs with a few simple divisions. In some lizards, like the Common chameleon (*Chamaeleo chameleon*) there are airsac dilatations caudally.
(c) Multicameral lungs are more advanced multichambered lungs with a single intrapulmonary bronchus.

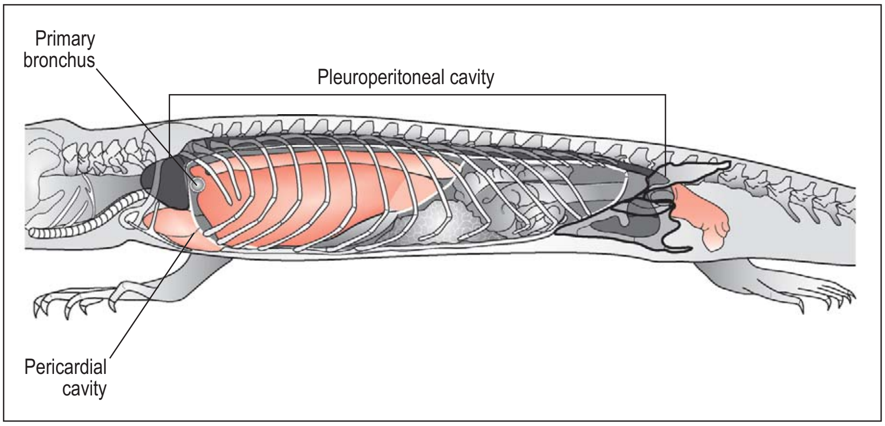


Figure 4.18 • Unicameral lizard – schematic diagram of celomic cavities (left lung, liver lobe and stomach removed). In primitive lizards, the lack of a postpulmonary septum results in their having an extensive combined pleuroperitoneal cavity. The heart is located cranially in the pectoral region.

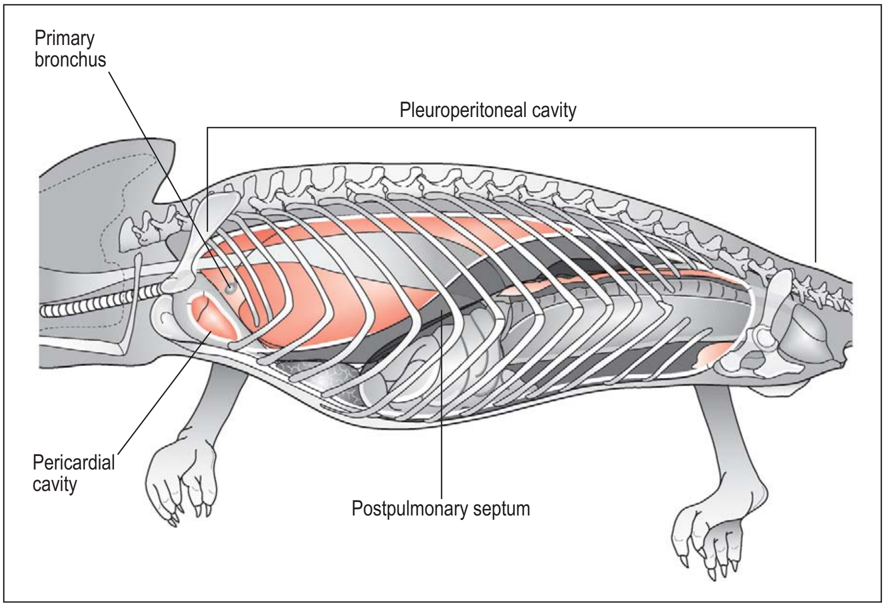


Figure 4.19 • Paucicameral lizard – schematic drawing (left lung, liver lobe and stomach removed) of celomic cavities showing small postpulmonary septum and partial separation between pleural and peritoneal cavities. The heart is located in the pectoral region.

Multicameral lungs

In the more advanced monitor lizards the postpulmonary septum completely divides the lungs in the pleural cavity from the peritoneal cavity. The lungs more closely resemble the lungs of primitive mammals and occupy the cranial dorsal and ventral cavity. As they have expanded cranioventrally the heart now occupies a more caudal position on the mid sternum rather than at the pectoral inlet. Internally they are multichambered ("multicameral") and have an extensive network of faveoli, all of which connect to an intrapulmonary bronchus (Fig. 4.20). Large volume and highly compliant lungs give an increased tidal volume and low respiratory rate (Bellairs 1969d; Bennett, AF 1972; Perry 1989; Perry & Duncker 1978).

Respiration cycle

Both inspiration and expiration are active processes that are followed by a non-ventilatory portion of varying length (up to 30 minutes in some species) (Wood & Lenfant 1976). Respiration is based on the negative celomic pressure that is produced by the intercostal muscles, aided by the trunk and abdominal muscles. In addition the lung walls contain smooth muscle that contracts and relaxes.

Like all reptiles, lizards have little capacity for aerobic respiration and switch to anaerobic quite fast; hence, they cannot sustain activity for long but work better in bursts. However, the large Australian Sand monitor (*Varanus gouldii*), has twice the aerobic capacity of other reptiles due to its highly developed lung falveoli and more myoglobin. This means it can sustain vigorous activity for longer without getting fatigued (Bennett, AF 1972).

CLINICAL NOTE

Lizards use the same intercostal muscles for breathing as for locomotion and so they actually cease breathing while running and then stop to breathe, which may explain why they are often active in short bursts (Pough 1998c).

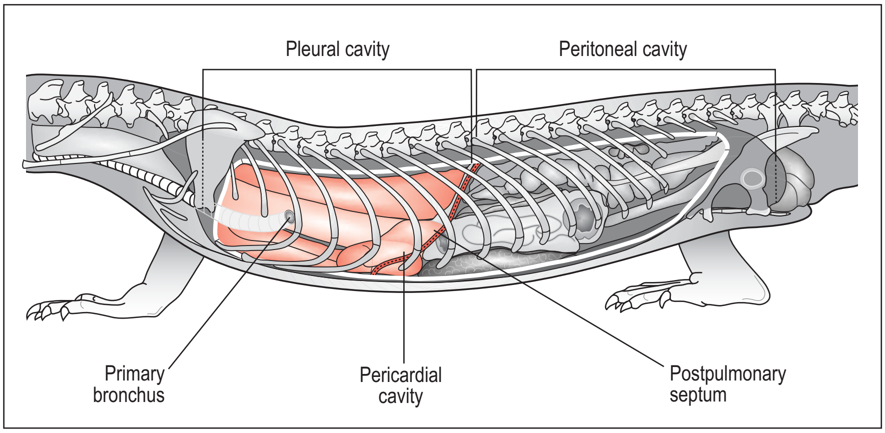


Figure 4.20 • Multicameral lizard (Monitor lizards) – schematic drawing showing complete separation of pleural from peritoneal cavities. This has allowed the lungs to expand cranially and ventrally causing the pericardial sac and heart to move caudally into the mid celom.

DIGESTIVE SYSTEM

The majority of lizards are omnivorous and carnivorous; only about 40 species are herbivorous and these tend to be larger in body size.

Prehension of food

Carnivorous lizards ingest their prey in two ways: small prey are seized and crushed by the jaws. Large prey are ingested by what is called *inertia feeding*. This is where the prey is lifted off the ground and shaken violently and then the jaws relax and slide forward over the inert prey item (Pough 1998e).

Dentition

Unlike snakes and chelonians, lizards do chew their food and will tear off pieces if the food item is too big to swallow. Lizard teeth are simple conical structures that have no sockets and are regularly shed and replaced in waves to always ensure there are adequate teeth for prehension of food. The replacement tooth is formed in the mucosa of the base, rather than below it as in mammals (Edmund 1970; King 1996b). Lizards can have either pleurodont or acrodont teeth (Fig. 4.21).

Pleurodont

Pleurodont teeth are attached to the inner sides of the mandible and are found in iguanids and varanids. These teeth are continually shed and replaced by new teeth forming at the lingual side of the base. The gingival margin is just behind the bony crest supporting the teeth (Edmund 1970; King 1996b).

CLINICAL NOTE

Iguanas have a rapid rate of teeth replacement. Each quadrant of their mouth has about 20 to 30 teeth and these are replaced up to five times a year, so a medium-sized iguana can replace 500 teeth a year!

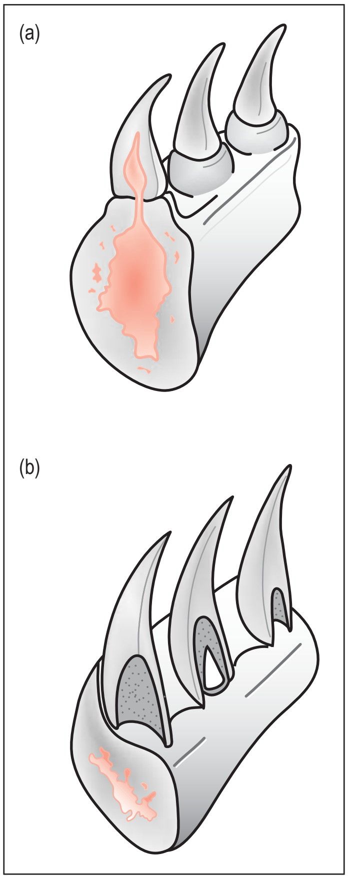


Figure 4.21 • Lizard dentition.
(a) Acrodonts, such as the agamids and chameleons, have the teeth attached to the biting edges of the mandible and maxilla.
(b) Pleurodonts, such as the iguanids and varanids, have the teeth attached to the inner sides of the mandible.

Acrodont

Acrodont teeth are attached to the biting edges of the mandible and maxillae and are found in agamids and chameleons. They are not replaced throughout life and wear with age, leaving the jaw to act as a cutting edge in the end. In most acrodont species (with the exception of the chameleon) the most rostral teeth are pleurodont (McCracken 1999).

Egg tooth

Newly hatched lizards have an egg tooth on the rostromedial side of the premaxilla. This is a modified premaxillary

CLINICAL NOTE

The gingival margin lies further back from the teeth in acrodont lizards, making species like Bearded dragons (*Pogona vitticeps*) and Water dragons (*Physignathus* spp.) more prone to periodontal disease if fed an inappropriate diet (McCracken 1999).

tooth and helps to slit the eggshell during hatching. Many species of gecko have a double egg tooth (Edmund 1970).

Venom

There are only two species of poisonous lizard: the Gila monster (*Heloderma suspectum*) and the Mexican Beaded lizard (*Heloderma horridum*), which come from the southwestern US and Mexico. Unlike snakes, the venom is located in large sublingual glands in the lateral lower jaw. The venom is secreted via ducts into the labial side of the mandible where adjacent grooved teeth transfer the neurotoxic venom (Barten 1996; Bellairs 1969c; Pough 1998e).

Tongue

The tongue is mobile and protrusible and attached to the hyoid apparatus at its base. It functions to bring scent particles to Jacobson's organ for olfaction, and for lapping, swallowing, and moving food through the oral cavity. Taste buds are poorly developed. In chameleons it is used for food prehension and the sticky tip can be projected rapidly over half the length of its body to catch prey (Liem et al. 2001). In monitors and tegus it is deeply forked and is used for exploring the environment, as in snakes. The Leopard gecko uses its mobile pink tongue to clean its corneas after feeding (Evans 1986).

CLINICAL NOTE

In the Green iguana the rostral tip of the tongue is a darker pink color but this should not be mistaken for a pathological lesion (Barten 1996).

Gastrointestinal tract

The gastrointestinal tract of insectivores and omnivores is relatively simple (Figs. 4.22 and 4.23). A short, thin-walled esophagus enters the stomach on the left side of the abdomen. The stomach is tubular and simple and leads into a short small intestine and large intestine. Unlike the avian gizzard the swallowing of stones to aid digestion is not normal behavior in lizards. Some species like geckos use their tail for fat storage as an emergency energy source (Fig. 4.24).

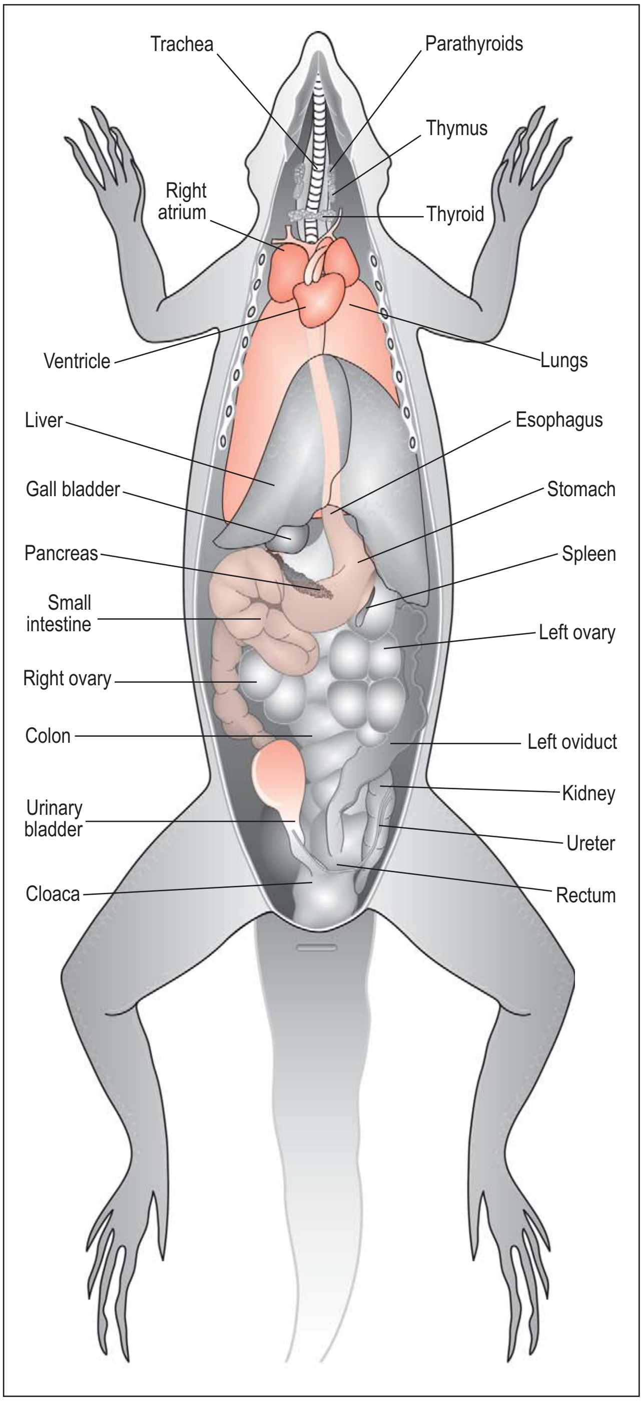


Figure 4.22 • Ventral view of female lizard showing internal anatomy.

CLINICAL NOTE

Lizards drink with their tongue, putting it slowly in and out of water, whereas snakes prefer to immerse their head in water and gulp it down.

Herbivores

Only about 3% of lizards are herbivorous (King 1996b) and most are found in the families Iguanidae (e.g., Green iguana)

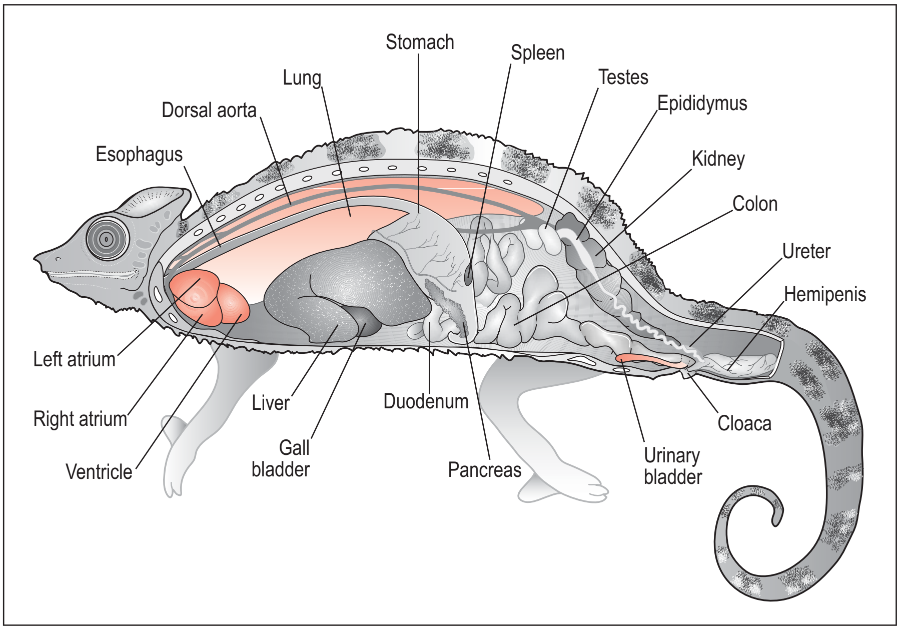


Figure 4.23 • Lateral, midsagittal view of male chameleon.

and Agamidae (e.g., Uromastyx). Many herbivores have blunt heads like tortoises, giving them powerful jaw musculature for mastication. Both pleurodont and acrodont teeth can occur. Unlike insectivores, which eat bite-sized insects, herbivores have to crop down pieces of vegetation and so use their teeth as if they were scissors. However, unlike in herbivorous mammals, chewing on one side cannot take place as the upper and lower jaws are the same width (King 1996b).

Herbivores such as the iguana are hindgut fermenters and are really only found in tropical areas where high ambient temperatures facilitate fermentation. The small intestine is short and the large intestine (cecum and colon) takes up 50% of the length. Protein and digestible nutrients are absorbed in the stomach and small intestine while the indigestible cellulose is broken down and absorbed as volatile fatty acids in the cecum and colon. Most herbivores have a large partitioned proximal colon which increases surface area and slows the passage of ingesta, thus giving more time for hindgut fermentation. The iguana has large transverse folds in the proximal colon (Fig. 4.25), subdividing it into five pockets which decrease in size distally, and can retain food there for up to 3½ days (King 1996b, 1996c; Troyer 1984).

Table 4.3 Examples of herbivorous lizards

Common name	**Scientific name**
Green iguana	*Iguana iguana*
Marine iguana	*Amblyrhynchus cristatus*
Common chuckwalla	*Sauromalus ater*
Solomon Island skink	*Corucia zebrata*
Spiny tailed lizard (Dab)	*Uromastyx acanthinurus*

Newly hatched iguanas have no microbial flora and in the wild they populate their gut by eating adult feces. They selectively eat more digestible proteins and have shorter transit times in order to gain enough energy for rapid growth (Troyer 1984).

Herbivorous species rely on high ambient temperatures and microorganisms to aid fermentation of cellulose into VFAs (King 1996b, 1996c). Total transit time is very slow in comparison to other non-ruminant herbivores. Mammals, from rabbits to elephants, take around 68 hours in comparison to up to 140 hours in the lizard. This is because reptiles do not ferment food during night cooling and have a much slower metabolism (Troyer 1984). It is also inversely related to body temperature (King 1996c).

URINARY SYSTEM

The kidneys are lobed and lie retroperitoneally within the pelvic canal in the dorsocaudal celom (Fig. 4.23). In some species the kidneys are fused in the midline. A short ureter drains the kidneys from the ventral side and opens via a urinary papilla in the urodeum. In male lizards this duct is an outgrowth of the vas deferens. Most lizards have a thin-walled bladder which arises from the ventral urodeum and extends forward under the coprodeum. Urine flows from the urodeum into the coprodeum (Fig. 4.26). In species without a bladder urine is stored and modified in the distal colon before being excreted (Davis et al. 1976).

Salt glands

Herbivorous lizards consume a lot of potassium in their diet and often have nasal salt glands to help them excrete the excess salts. They also excrete potassium urate salts in higher concentration in their urine (Dunson 1976).

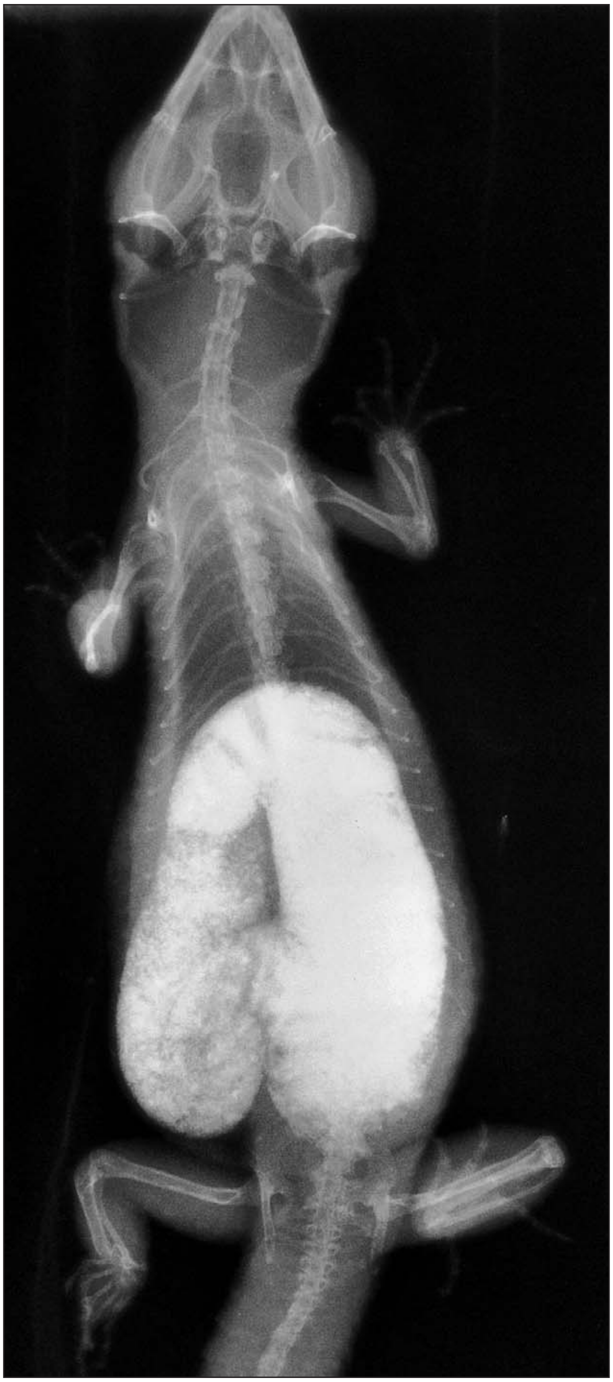


Figure 4.24 • Radiograph of Leopard gecko (*Eublepharis macularius*) with colonic impaction due to substrate ingestion. There is loss of soft tissue opacity from the tail base (normally a site of fat storage in many geckos) indicating emaciation.

CLINICAL NOTE

Nephromegaly can result in obstruction of the colon as it passes between the kidneys. This is quite common in aged green iguanas (Barten 1996).

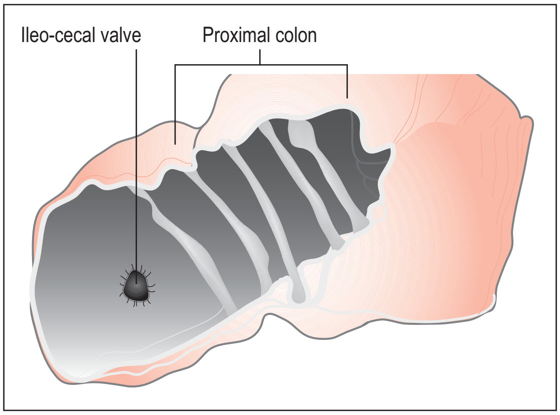


Figure 4.25 • Diagram of iguana colon showing large transverse folds in the proximal colon subdividing it into five pockets. Food can be retained there for up to 3½ days.

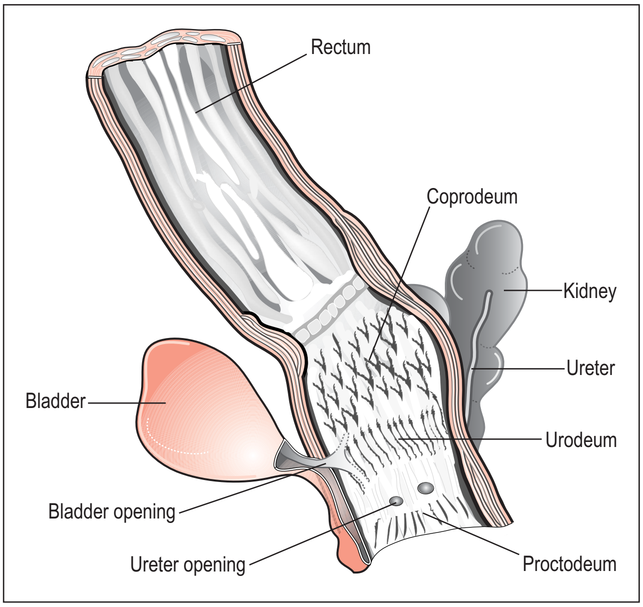


Figure 4.26 • Distal colon and cloaca of lizard with bladder. Urine empties from the ureter into the urodeum and is then refluxed into the bladder.

REPRODUCTIVE SYSTEM

Breeding season

In many lizards from temperate climates the gonads reach maximum size on emergence from hibernation and are smallest during the summer months. In tropical climates the breeding season coincides with the start of the wet season, so there is moisture for egg incubation and an abundant food supply for hatchlings (DeNardo 1996).

Male

The testes are located cranial to the kidneys and attached to the dorsal wall by a mesorchium. In some species of male lizard, the kidney has a posterior sexual segment that becomes swollen

SEXUAL DETERMINATION

- Sexual dimorphism – Many adult species are sexually dimorphic with males being more brightly colored and often possessing crests, throat fans, etc. The male iguana has taller dorsal spines and larger dewlaps; male chameleons have elaborate horns, crests, and plates on their head. Femoral or pre-cloacal pores are also more prominent in the males (DeNardo 1996) (Fig. 4.27).
- Sexual probes – These can be used but are not as accurate as in snakes.
- Eversion of the hemipenes – This can be done by injecting saline into the cloaca in species like monitors, tegus, and large skinks, which are difficult to sex (DeNardo 1996).
- Endoscopy – This can be used to examine the gonads.
- Radiography – The hemipenes of some male monitor lizards can calcify and be seen on radiographs.
- Ultrasonagraphy – This can be used to examine the hemipenes or ovaries/follicles.

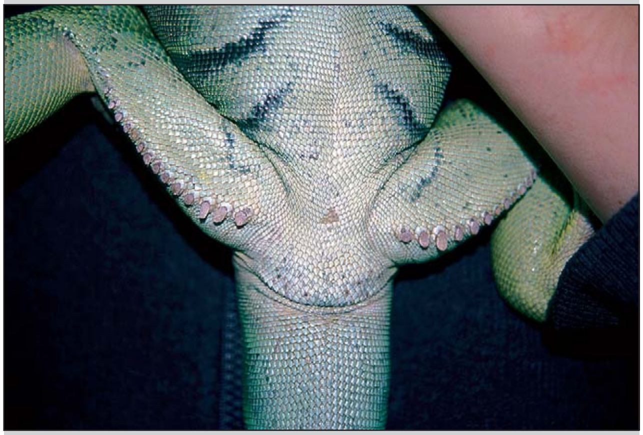


Figure 4.27 • View of medial hindlimbs of Green iguana (*Iguana iguana*) showing prominent femoral pores in the male.

CLINICAL NOTE

The adrenal glands are suspended in the mesovarium and mesorchium so must be carefully avoided during neutering. The right testis is intimately associated with the vena cava so ligation is best achieved with surgical hemoclips.

during the breeding season and contributes to seminal fluid. The right testis lies cranial to the left and is intimately connected with the vena cava by short blood vessels of 1–2 mm. The left testis has its own testicular blood vessels which lie close to the left adrenal gland (Bennett & Mader 1996) (Fig. 4.28).

The male has paired hemipenes, which are stored in the tail base and can be visualized externally by bulges at the ventral proximal tail. Only one hemipene is used during copulation. The organ is erected by vascular engorgement and muscular action and everted to protrude through the cloaca. Sperm passes from the vas deferens into the male urodeum and is then carried in a groove down the hemipene to be deposited into the female cloaca (Bellairs 1969g).

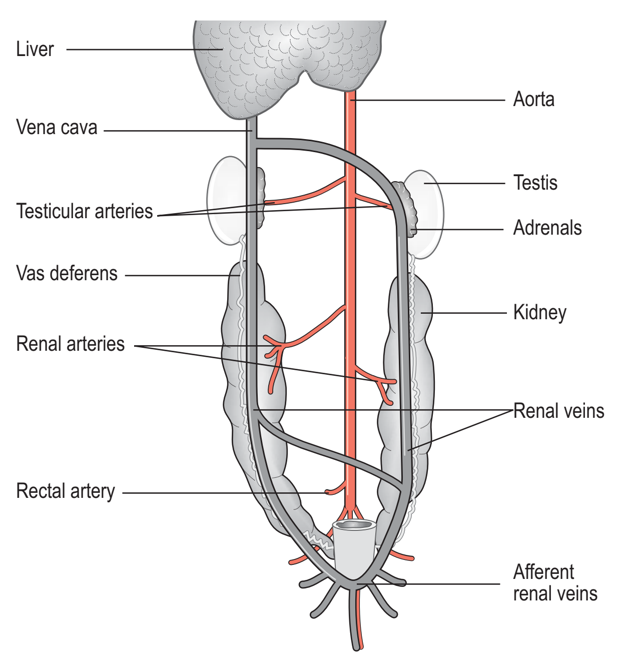


Figure 4.28 • Location of testes and kidneys in the male lizard.

CLINICAL NOTE

The hemipene is solely an organ of reproduction; hence, amputation of prolapsed hemipenes is possible if they are non viable and cannot be replaced internally (Fig. 2.12).

Female

The female has paired ovaries and oviducts, which lie at the same level cranial to the kidneys (Fig. 4.29). The ovary consists of a cluster of oocytes lines by a thin mesovarium. The oviduct is pleated and has a wide infundibulum. As with the testes, the right ovary lies close to the vena cava and is attached to it by tiny blood vessels. The left ovarian blood supply lies close to the left adrenal gland (Bennett & Mader 1996).

CLINICAL NOTE

When ovulation does not occur the mature follicle remains causing preovulatory retention or follicular stasis. Postovulatory retention is when the ova lies within the oviduct and the lizard is egg bound (Barten 1996).

Oviparity

In oviparous species the eggs are retained within the mother until birth. This is the more usual state for lizards and is

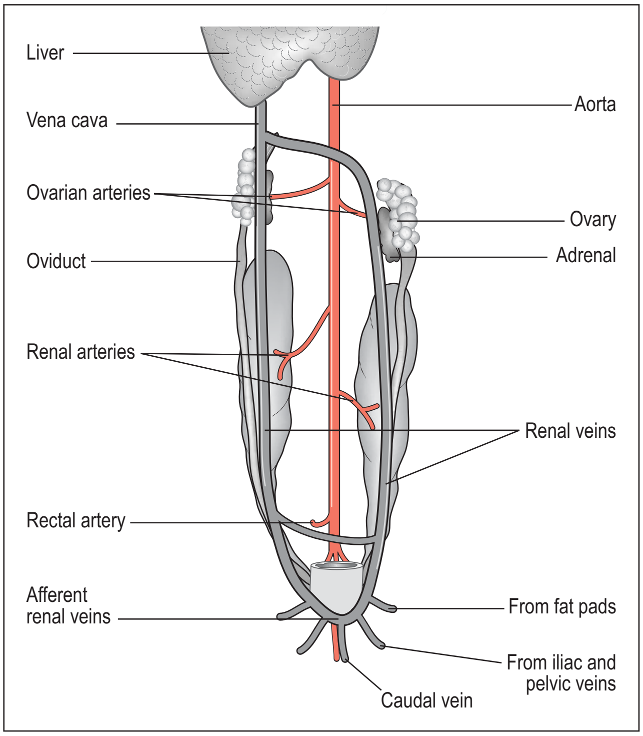


Figure 4.29 • Location of ovaries and kidneys in the female lizard.

seen in Gekkonidae and Iguanidae. The normal clutch size is from 3 to 15. Eggs are covered by a leathery shell and can appear a bit shrunken when laid (Bellairs 1969g; DeNardo 1996; Palmer et al. 1997; Pough 1998b; Thompson 1997).

Viviparity

About one fifth of lizards are viviparous. The fetus is retained within the oviduct where there is a primitive placental type of circulation. The common European lizard (*Lacerta fragilis*) is viviparous (Bellairs 1969g; DeNardo 1996; Palmer et al. 1997; Thompson 1997).

GENERAL INTEREST

A few species of lizards are parthenogenic. These lay unfertilized eggs that produce only female young, genetically identical to the parent. This "virgin birth" can occur in some Asian lacertids (*Lacerta* spp.) and North American whiptails (Aspidoscelis, prev. Cnemidophorus) (Evans 1986).

SENSES

Parietal eye

The parietal eye (sometimes incorrectly called the pineal eye because the nerve connecting the parietal gland to the brain enters at the base of the pineal gland) is well developed in some species like the Green iguana (*Iguana iguana*). It is located on the dorsal midline of the head, beneath the skin in the parietal foramen, and consists of a degenerate eye containing a lens and retina. Although it does not form images it connects with the pineal gland and may play a role in thermoregulation, reproduction, and basking time (Evans 1986; Firth & Turner 1982).

Hearing

There is no external ear apart from a fold of skin in some species (Fig. 4.30) and the tympanic membrane is usually visible in a shallow depression on the side of the head (Murray 1996). In some species it is covered with a thin transparent membrane, the outer layer of which is shed during ecdysis. Airborne vibrations are picked up by these membranes and transmitted via the columella to the inner ear. Hearing is better than in snakes and chelonians but sensitive to only a narrow range of low-frequency sounds. Geckos have the best hearing of all lizards, which may fit in with the fact that they are also the most vocal. Some burrowing lizards have no external or middle ear but, like snakes, transmit sound by bone conduction (Baird 1970; Bellairs 1969f; Murray 1996).

Some gecko species (*Phelsuma* spp.) store calcium in endolymphatic sacs which can appear as white swellings on either side of the neck. This calcium can be mobilized for egg laying.

Sight

The majority of lizards are insectivorous so need keen eyesight to catch prey. Lizards have good color vision but only a narrow binocular field, so this is why they typically cock their head to one side to get the best monocular vision. Chameleons have the best vision of all, having excellent binocular and monocular vision (Bellairs 1969f).

A thin interorbital septum separates the large orbits. As in chelonians the sclera is supported by a ring of small bones called ossicles. This allows for attachment of ciliary muscles and keeps the shape of the globe (Underwood 1970).

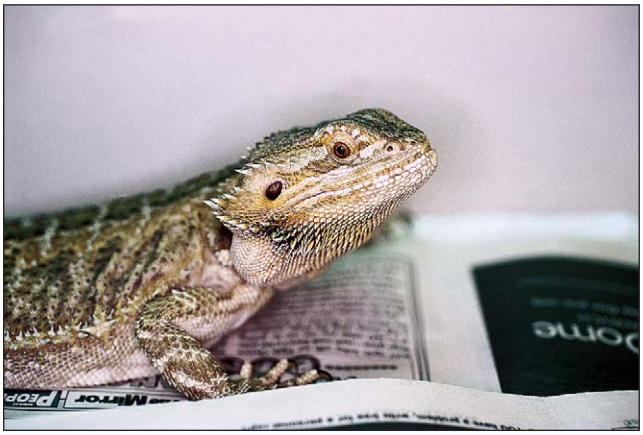


Figure 4.30 • Bearded dragon (*Pogona vitticeps*) showing lack of external ear.

External adnexa

Eyelids are present, except in some gecko species. [The very popular Leopard gecko (*Eublepharis macularis*) does have movable eyelids.] As in birds, the eyelids are unequal in size. The upper lid has little mobility so it is the lower lid which moves upward to cover the majority of the surface of the eye. In some species this can be transparent so some vision is possible even when the eye is closed. A nictitating membrane is present with a Harderian gland opening medially. Two lacrimal canaliculi are present at the rostromedial margins of the lower lid (Bellairs 1969f; Underwood 1970).

The pupil is usually round and relatively immobile in diurnal species but slit-like in nocturnal species. Many geckos have a serrate pupillary opening that results in a series of small holes when the pupil is completely closed. The retina of diurnal lizards has only cones, whilst nocturnal geckos have more rods. The highly vascular conus papillaris (similar to the pecten of birds) originates from the head of the optic nerve (Williams 1996). A *fovea centralis*, a depression in the retina, gives acute vision and is often present in diurnal species (Barten 1996).

CLINICAL NOTE

Some lizards like the Tokay gecko (*Gekko gecko*) and the oscellated skinks (*Ablepharus* spp.) have fused eyelids that form a spectacle, as in snakes (Bellairs 1969f; Williams 1996). In these species the lacrimal glands secrete into the subspectacular space, which is then drained by the nasolacrimal duct. Infections here can lead to subspectacular abscesses where the fluid cannot drain away.

Olfaction

The Jacobson's organ located in the roof of the mouth is highly sensitive and innervated by a branch of the olfactory nerve. The tongue is used as an organ of both taste and smell (Parsons 1970).

KEY POINTS

- Large ventral abdominal vein
- Acrodont or pleurodont teeth
- Herbivorous species have large colon and slower gut transit times
- Good hearing and vision

INTEGUMENT

A mainly terrestrial animal like the lizard has scales to protect itself from desiccation. These scales are formed by the folding of the epidermis and contain keratin, which provides the water-conserving properties. In some species like skinks (*Scincidae* spp.) the scales are attached to underlying dermal bony plates called *osteoderms*, which give added protection and support and which are identifiable on radiographs (Bellairs 1969e; Lillywhite & Maderson 1982).

CLINICAL NOTE

These osteoderms can appear like radiopaque densities on radiographs and should not be confused with lung metastases.

Scales can be modified into crests, sharp spines, dewlaps and shields for sexual display or territorial conflict. In between the scales, the skin is thin and folded to allow for expansion (hinges or scale pockets). The dermis contains the chromatophores, which provide the elaborate range of skin coloration, most particularly notable in the chameleon.

Ecdysis

At ecdysis, scales are shed piecemeal and many lizards will rub against hard objects to shed the molting layer. Many show altered behavior like hiding away, cessation of eating, and fading of color (Fig. 4.31). Many lizards also use a swell mechanism to help the dead skin slough off. This is when venous return to the heart is restricted by muscles constricting the internal jugular vein. This causes the head to bulge, particularly around the eyes which have large venous sinuses. Other lizards are also capable of inflating their bodies with air (Bellairs 1969e; Evans 1986; Perry & Duncker 1978; White 1976).

Skin glands

The skin has few glands but many lizards like the Green iguana have femoral pores in a single row on the ventral aspect

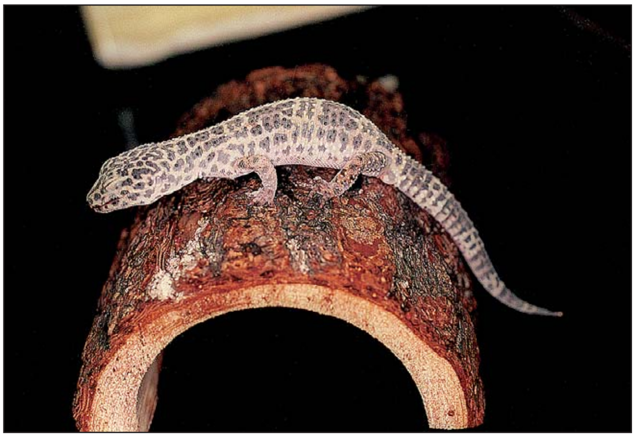


Figure 4.31 • Leopard gecko (*Eublepharis macularius*) about to shed.

of the thigh. These are not true glands but are tubular skin invaginations that produce a waxy secretion. They are larger and more developed in the male and can be helpful in sexual determination. Many gecko species also have precloacal pores, which lie in a v-shaped row anterior to the cloaca and are more pronounced in males.

REFERENCES

Baird, I. L. (1970) The anatomy of the reptilian ear. In C. Gans (ed.), *Biology of the reptilia*. Vol. 2, Morphology B. London: Academic Press. pp. 193–272.

Barten, S. L. (1996) Biology – lizards. In D. R. Mader (ed.), *Reptile medicine and surgery*. Philadelphia: WB Saunders. pp. 47–61.

Bellairs, A. (1969a) *The life of reptiles*. Vol. 1. London: Weidenfeld and Nicolson. Body form, skeleton and locomotion; pp. 44–116.

Bellairs, A. (1969b) *The life of reptiles*. Vol. 1. London: Weidenfeld and Nicolson. Feeding and cranial mechanics; pp. 116–184.

Bellairs, A. (1969c) *The life of reptiles*. Vol. 1. London: Weidenfeld and Nicolson. The venom apparatus and venom; pp. 184–217.

Bellairs, A. (1969d) *The life of reptiles*. Vol. 1. London: Weidenfeld and Nicolson. The internal economy; pp. 217–282.

Bellairs, A. (1969e) *The life of reptiles*. Vol. 2. London: Weidenfeld and Nicolson. The skin; pp. 283–332.

Bellairs, A. (1969f) *The life of reptiles*. Vol. 2. London: Weidenfeld and Nicolson. Nervous system, psychology and sex organs; pp. 332–390.

Bellairs, A. (1969g) *The life of reptiles*. Vol. 2. London: Weidenfeld and Nicolson. Sex and reproduction; pp. 390–433.

Bellairs, A. (1969h) *The life of reptiles*. Vol 2. London: Weidenfeld and Nicolson. Growth, age and regeneration; pp. 458–488.

Bellairs, A. D., & Bryant, S.V. (1985) Autotomy and regeneration in reptiles. In C. Gans & F. Billett (eds.), *Biology of the Reptilia*. Vol 15, Development B. New York: Wiley Interscience. pp. 302–350.

Bennett, A. F. (1972) The effect of activity and oxygen consumption, oxygen debt and heart rate in lizards *Varanus gouldii* and *Sauromalus hispidis*. *Journal of Comparative Physiology 79*, 259–280.

Bennett, R. A. (1996) Neurology. In D. R. Mader (ed.), *Reptile medicine and surgery*. Philadelphia: WB Saunders. pp. 141–148.

Bennett, R. A., & Mader, D. R. (1996) Soft tissue surgery. In D. R. Mader (ed.), *Reptile medicine and surgery*. Philadelphia: WB Saunders. pp. 287–298.

Davis, L. E., Schimdt-Nielson, B., & Stolte, H. (1976) Anatomy and ultrastructure of the excretory system of the lizard, *Sceloporus cyanogenys*. *Journal of Morphology 149*, 279–326.

DeNardo, D. (1996) Reproductive biology. In D. R. Mader (ed.), *Reptile medicine and surgery*. Philadelphia: WB Saunders. pp. 212–224.

Dunson, W. A. (1976) Salt glands in reptiles. In C. Gans & W. R. Dawson (eds.), *Biology of the reptilia*. Vol. 5, Physiology A. London: Academic Press. pp. 413–441.

Edmund, A. G. (1970) Dentition. In C. Gans (ed.), *Biology of the reptilia*. Vol. 1, Morphology A. London: Academic Press. pp. 117–194.

Evans, H. E. (1986) Reptiles – Introduction and anatomy. In M. E. Fowler (ed.), *Zoo and wild animal medicine*, 2nd edn. Philadelphia: WB Saunders. pp. 108–132.

Firth, B. J. & Turner, J. S. (1982) Sensory, neural and hormonal aspects of thermoregulation. In C. Gans & F. H. Pough (eds.), *Biology of the reptilia*. Vol. 12, Physiology C. London: Academic Press. pp. 213–259.

King, G. (1996a) *Reptiles and Herbivory*. London: Chapman & Hall. Reptiles and Herbivory, C ; pp. 1–23.

King, G. (1996b) *Reptiles and Herbivory*. London: Chapman & Hall. Lizards; pp. 29–42.

King, G. (1996c) *Reptiles and Herbivory*. London: Chapman & Hall. Turtles and tortoises; pp. 47–60.

King, G. M., & Custance, D. R. (1982) *Colour atlas of vertebrate anatomy*. Oxford: Blackwell Scientific. The lizard; pp. 4.1–4.10.

Liem, K. F., Bemis, W. E., Walker, W. F., & Grande, L. (eds.) (2001) *Functional anatomy of the vertebrates*, 3rd edn. Fort Worth, Tex.: Harcourt College. The digestive system: Oral cavity and feeding mechanisms; pp. 532–556.

Lillywhite, H. B., & Maderson, P. F. (1982) Skin structure and permeability. In C. Gans & F. H. Pough (eds.), *Biology of the reptilia*. Vol. 12, Physiology C. London: Academic Press. pp. 397–433.

McCracken, H. E. (1999) Periodontal disease in lizards. In M. E. Fowler & R. E. Miller (eds.), *Zoo & wild animal medicine*: *Current therapy*, 4th edn. Philadelphia: WB Saunders. pp. 252–259.

Murray, M. J. (1996) Aural abscess. In D. R. Mader (ed.), *Reptile medicine and surgery*. Philadelphia: WB Saunders. pp. 349–352.

Murray, M. J. (2000) Reptilian blood sampling and artifact considerations. In A. Fudge (ed.), *Laboratory medicine – avian and exotic pets*. Philadelphia: WB Saunders. pp. 185–191.

Palmer, B., Uribe, M. C. et al. (1997) Reproductive anatomy and physiology. In L. Ackermann (ed.), *The biology, husbandry and healthcare of reptiles*. Vol. 1, The biology of reptiles. N.J.: TFH Publications. pp. 54–81.

Parsons, T. S. (1970) The nose and Jacobson's organs. In C. Gans (ed.), *Biology of the reptilia*. Vol. 2, Morphology B. London: Academic Press. pp. 99–185.

Perry, S. F. (1989) Structure and function of the reptilian respiratory system. In S. C. Wood (ed.), *Comparative pulmonary physiology – current concepts*. New York: Dekker. pp. 193–237.

Perry, S. F., & Duncker, H. R. (1978) Lung architecture, volume and static mechanics in five species of lizards. *Respiratory Physiology 34*, 61–81.

Pough, F. H., Andrew, R. M., Cadle, J. E. et al. (1998a) *Herpetology*. Englewood Cliffs, N.J: Prentice Hall. Herpetology as a field of study; pp. 1–20.

Pough, F. H., Andrew, R. M., Cadle, J. E. et al (1998b) *Herpetology*. Englewood Cliffs, N.J: Prentice Hall. Classification and diversity of extant reptiles; pp. 75–133.

Pough, F. H., Andrew, R. M., Cadle, J. E. et al. (1998c) *Herpetology*. Englewood Cliffs, N.J: Prentice Hall. Energetics and performance; pp. 173–204.

Pough, F. H., Andrew, R. M., Cadle, J. E. et al, (1998d) *Herpetology*. Englewood Cliffs, N.J: Prentice Hall. Body support and locomotion; pp. 235–265.

Pough, F. H., Andrew, R. M., Cadle, J. E. et al. (1998e) *Herpetology*. Englewood Cliffs, N.J: Prentice Hall. Feeding; pp. 267–305.

Pough, F. H., Janis, C. M., & Heiser, J. B. (2002) *Vertebrate life*, 6th edn. Englewood Cliffs, N.J: Prentice Hall. The lepidosaurs: Tuatara, lizards and snakes; pp. 294–341.

Redrobe, S., MacDonald, J. (1999) Sample collection and clinical pathology of reptiles: Clinical pathology and sample collection. In D. R. Reavill (ed.), The Veterinary Clinics of North America:

Exotic animal practice. Vol. 2. Philadelphia: WB Saunders. pp. 709–730.

Thompson, M. B. (1997) Egg physiology and biology. In L. Ackermann (ed.), *The biology, husbandry and healthcare of reptiles*. Vol. 1, The biology of reptiles. N.J: TFH Publications, pp. 88–121.

Troyer, K. (1984) Structure and function of the digestive tract of a herbivorous lizard *Iguana iguana*. *Physiological Zoology 57*(1), 1–8.

Uetz, P. (2000) How many reptile species? *Herpetology Review 31*, 13–15.

Underwood, G. (1970) The eye. In C. Gans (ed.), *Biology of the Reptilia*. Vol. 2, Morphology B. London: Academic Press. pp. 1–93.

White, F. N. (1976) Circulation. In C. Gans & W. R. Dawson (eds.), *Biology of the reptilia*. Vol. 5, Physiology A. London: Academic Press. pp. 275–328.

Williams, D. L. (1996) Opthalmology. In D. R. Mader (ed.), *Reptile medicine and surgery*. Philadelphia: WB Saunders. pp. 175–185.

Wood, S. C., & Lenfant, C. J. (1976) Respiration: Mechanics, control and gas exchange. In C. Gans & W. R. Dawson (eds.), *Biology of the reptilia*. Vol. 5, Physiology A. London: Academic Press. pp. 225–267.

5

Snakes

INTRODUCTION

Although snakes today invoke fear and phobias in many people they were highly revered in the ancient world. The fact they could disappear for the winter and emerge fresh and renewed in the spring meant they were seen to be immortal and worshipped as a symbol of healing and renewal. The Australian aborigines worshipped the Rainbow serpent and saw her as a symbol of water and life. Alexander the Great claimed he was conceived by Zeus in the guise of a snake and used them as a symbol of his power. Aesculapius, the Greco-Roman god of healing was portrayed as a man carrying a wooden staff entwined by a snake, and this emblem is still the symbol of modern medicine today. It was later, with the advent of Christianity, that snakes became the scapegoat for paganism; the snake became the evil serpent luring Adam and Eve away from paradise and the forked tongue became synonymous with deceit.

Snakes evolved from lizards, which have a short trunk (snout to vent) and long tail. During the process of elongation, snakes developed the converse of this and have a long trunk with a short tail. They occur widely around the world, only being absent from polar and high-altitude regions where permafrost prevents them from hibernating. However, the majority are found in equatorial tropical rainforest where the abundance of food, high humidity and temperature provides the ideal habitat. In temperate climates, like North America and Europe, snakes hibernate during the cold months (Evans 1986).

Size

Snakes can vary greatly in size. At one extreme are the giant species like the Green anaconda (*Eunectes murinus*), which can grow to 10 m, and the equally long but less wide in girth Reticulated python (*Python reticulatus*). At the other are the smallest snakes, which are the secretive and burrowing blind snakes (*Typhlopidae*), measuring only 10–30 cm (Bellairs 1969h).

Longevity

Snakes like pythons and boas can live for as long as 20–30 years, and colubrids live for about 20 years.

TAXONOMY

Many families of snakes include primitive blind, burrowing species not commonly seen as pets. Others include only one species. This book will refer to only four major families: Boidae, Colubridae, Elapidae, and Viperidae. The Boidae and Colubridae contain the species most commonly seen in veterinary practice.

Table 5.1 Examples of common snake families

Family	Common name	Approx. no. of species	Species examples
Viperidae	Viper	227	Rattlesnake, Pit viper, Puff adder
Elapidae		290	Mamba, Cobra, Tigersnake, Brownsnake, Taipan, Sea snake
Colubridae	Typical snakes	1700	Boomslang, Cornsnake, Rat snake, Kingsnake, Milksnake, Garter snake
Boidae		63	Boa constrictor, Anaconda, Royal python

Boidae

These include the giant snakes, such as the anaconda and reticulated python. There are two main groups – the boas, which are viviparous and come from North, South, and Central America, and the oviparous pythons from Africa, Asia, and Australia.

These are powerful constricting snakes, which are often popular pets due to their docility. They are the most primitive of snakes, having vestigial spurs, two carotid arteries, and a coronoid bone (this part of the jawbone is absent in the more advanced species). They also have two lungs, some possess a cecum, and have shorter tails. Many have specialized infrared pit receptors on the upper and lower labial scales (Bellairs 1969d; Pough 1998a).

Colubridae

This family are the so-called typical snakes and comprises 70% of snake species (1700 species) (Pough 1998a). These are the most widely distributed (although they are not found in Australia) and are especially common in North America. They range from arboreal to aquatic to terrestrial. Some species, like the Boomslang (*Dispholidus typus*), are rear fanged but most species are harmless. These more advanced snakes have evolved to having only one functional right lung and a single left carotid artery.

Elapidae

These snakes are closely related to the colubrids but are probably more advanced. They have small heads and front fangs and include some particularly venomous species, such as the cobras and mambas. The group includes a lot of Australian species which have filled niches not occupied by vipers and colubrids. They are mostly oviparous. Like the colubrids, they have only one functional right lung and a single left carotid artery (Pough 1998a).

Viperidae

The vipers are the most advanced snakes in evolutionary terms and are found everywhere except Australia because they evolved after that landmass broke away. They tend to be short and stocky, with broad heads and may be oviparous or viviparous. The have only one carotid artery, one right lung, and a short hinged maxilla that allows the front fangs to be erected. The subfamily Crotalinae, which includes pit vipers and rattlesnakes, have heat-sensitive receptors between the eyes and nostrils. The rattlesnake has a rattle composed of keratin left over after shedding (Pough 1998a).

THERMOREGULATION

The optimum temperature range for snakes is 18–34° C. Temperate snakes have a preferred body temperature of 24° C and tropical snakes favor around 28° C. Heat stress occurs at 35° C and death at 38–44° C. When the temperature drops to 10° C the snake goes into torpor and will die if it is reduced to below 4° C.

The tropical regions provide ideal temperatures for snakes and this is why the greatest variety of diurnal and nocturnal species are found there. In temperate climates snakes are usually diurnal, basking in the morning sun to heat up and hibernating in winter. Subtropical snakes spend the hottest part of day under the substrate. In times of drought when food and water is scarce the snake will estivate to conserve water.

Their length enables snakes to have regional differences in body temperatures. Snakes have a very high ratio of surface area to body mass when uncoiled and so lose heat rapidly. When coiled this minimizes surface area to mass and this enables heat to be conserved.

GENERAL EXTERNAL ANATOMY

The cross-section of snakes can vary from circular to triangular to ovoid, depending on the habitat. The belly is always slightly flattened to aid locomotion. The single ventral scales are called “gastropeges” and the scales caudal to the vent are simply called “subcaudal scales”. Arboreal snakes like constrictors have quite a prehensile tail.

Most snakes use color to camouflage themselves or to give warning signals. Snakes that live among foliage are often green whereas desert species are often yellow to red to match the sand. The venomous coral snakes (*Micrurus species*) have vivid bands of color to warn prey. “False” coral snakes such as the Milksnake (*Lampropeltis triangulum*) use the same mimicry to keep prey away, even though they are not venomous.

GENERAL INTERNAL ANATOMY

The snake has evolved its body for crawling so has few external features. Elongation has also resulted in asymmetry of viscera with right-sided organs lying cranial to and being larger than left (Fig. 5.1). To explain the location of organs more easily it is best to divide the length of the snake roughly into three regions. The cranial region has the heart, trachea, esophagus, thyroid and proximal lung. The middle region has the stomach, liver, lung, spleen, and pancreas. The caudal region has the small and large intestines, kidneys and gonads.

Cranial third

In all species of snake the heart lies cranioventral to the termination of the trachea, although it is mobile to allow for the passage of large food items. The thyroid gland is just cranial to the heart. The thymus gland (which does not involute in adults) is thin and lies on the trachea proximal to this. The rostral parathyroids lie near the angle of the jaw while the caudal pair lies near the thymus, just rostral to the heart (McCracken 1999) (Figs. 5.2 and 5.3).

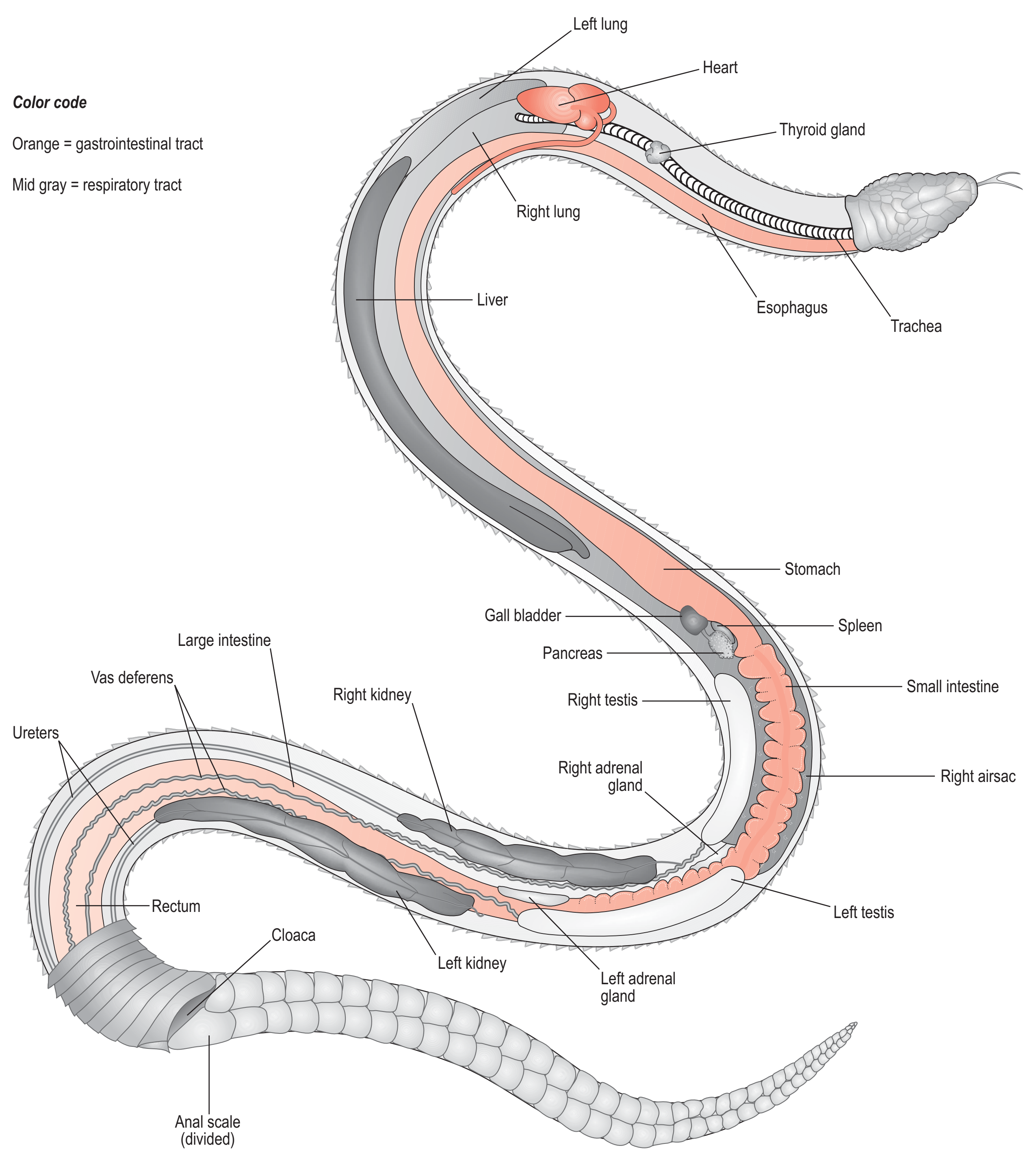

Color code
Orange = gastrointestinal tract
Mid gray = respiratory tract
Left lung
Heart
Thyroid gland
Right lung
Liver
Esophagus
Trachea
Stomach
Gall bladder
Spleen
Pancreas
Small intestine
Large intestine
Vas deferens
Right kidney
Right testis
Ureters
Right adrenal gland
Right airsac
Rectum
Cloaca
Left kidney
Left testis
Left adrenal gland
Anal scale (divided)

Figure 5.1 • Internal anatomy of the snake (male) – the celomic fat pads have been removed to show caudal viscera. Note the location of the gall bladder some distance from the liver.
Colour code
Orange = gastrointestinal tract
Mid gray = respiratory tract

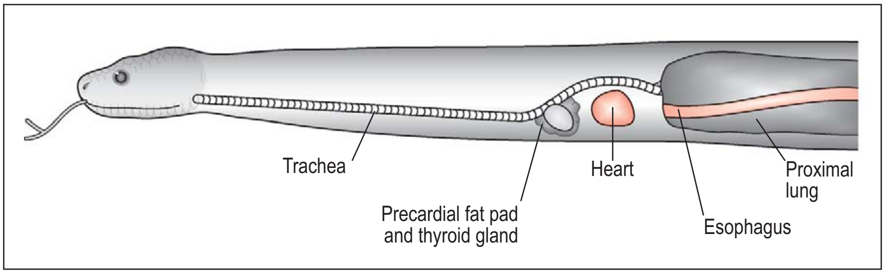

Trachea
Precardial fat pad and thyroid gland
Heart
Proximal lung
Esophagus

Figure 5.2 • Internal anatomy of cranial third showing location of trachea, thyroid, heart, proximal lung (right) and esophagus.

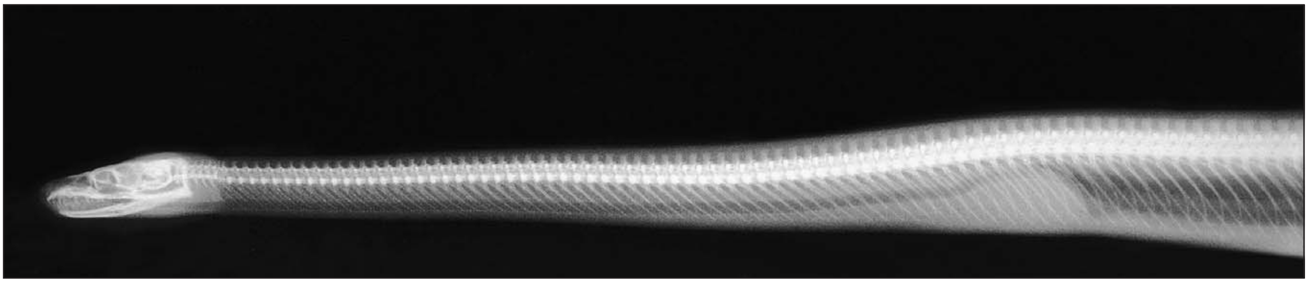


Figure 5.3 • Lateral radiograph of cranial third of the snake.

Middle third

The gall bladder lies near the pylorus of the stomach and is located some distance from the posterior pole of the liver. In some species the spleen and pancreas are fused into a splenopancreas and lie adjacent to the gall bladder, forming an organ triad. The right ovary lies either near to this triad or just caudal to it (McCracken 1999) (Figs. 5.4 and 5.5).

Caudal third

The right and left gonads occur in sequence, followed by the right and left kidneys. The pink adrenal glands can be visualized medial to the respective gonads and lie in the mesorchium/mesovarium. The intestines are linear and in Boidae a cecum is visible at the junction of the small intestine and colon. Celomic fat bodies lie ventral to all the

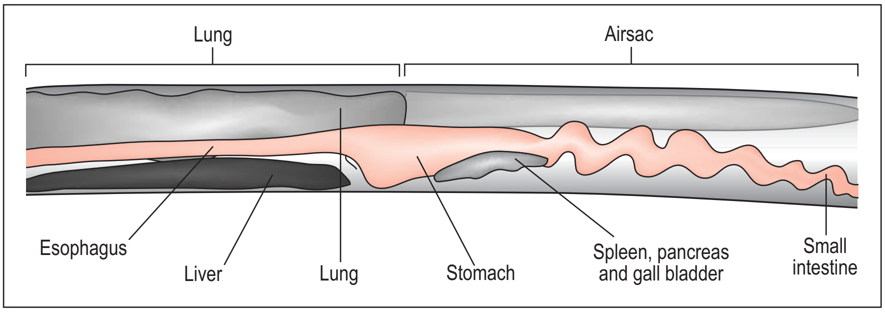

Lung
Airsac
Esophagus
Liver
Lung
Stomach
Spleen, pancreas and gall bladder
Small intestine

Figure 5.4 • Internal anatomy of middle third of the snake showing liver, lung, stomach, spleen, and pancreas.

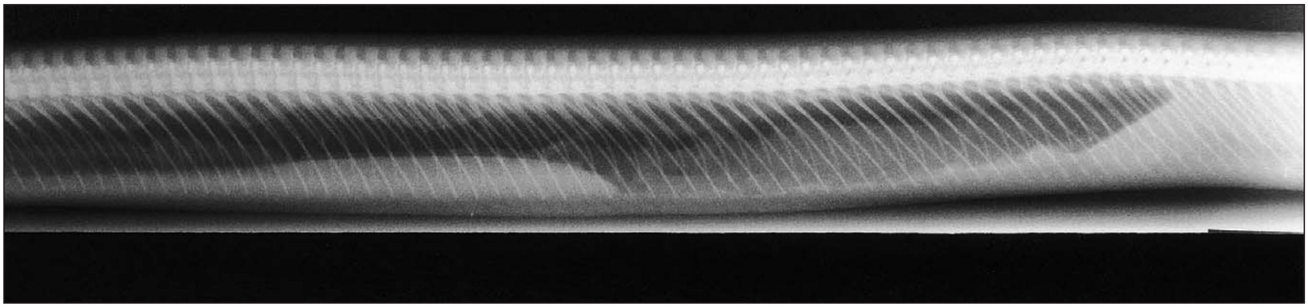


Figure 5.5 • Radiograph of middle third of the snake.

viscera, starting at the level of the gall bladder and extending caudally to the level of the cloaca (McCracken 1999) (Figs. 5.6 and 5.7).

SKELETAL SYSTEM

Skull

The snake has the most kinetic skull of all, with extremely flexible and mobile bones in all parts. It has no temporal arch, interorbital septum or middle ear cavity. Instead, its intricate design enables a reptile with a small mouth to eat enough large prey to sustain its length. The skull is modified so that all the tooth-bearing bones of the skull are able to move independently; the braincase is heavily ossified to protect it from protesting prey (Liem et al. 2001a) (Fig. 5.8).

Snakes have no mandibular symphysis; instead, flexible skin allows the jaw bones to move apart and forward or backward (Figs. 5.9 and 5.10). The quadrate bone which articulates with the lower jaw and palatomaxillary arch also has a very loose articulation. This becomes rigid when under tension but extremely flexible when relaxed (Fig. 5.10). More advanced viperid snakes have elongate quadrate bones slanting backwards and outwards giving them the notorious triangular shaped head. Many also have an articulation between the prefrontal and maxillary bones (Bellairs 1969b; Pough 1998a; Pough et al. 2002) (Fig. 5.11).

Each half of the skull works separately and this independence allows the snake to literally walk its jaw along large prey (Fig. 5.12). The left half of the upper and lower jaw can be moved and then clamped allowing the right side to advance forwards. Snakes often yawn after a meal to allow their jawbones to reposition themselves.

Vertebrae

There are often up to 400 vertebrae precloacally, each with its own pair of ribs and large axial skeletal muscles. Each vertebra has five separate articulations with its fellow vertebrae and this, combined with the large number of vertebrae, results in a very flexible backbone (Hoffstetter & Gasc 1970). The hypaxial and epaxial muscles extend along these vertebrae by an interlocking system of muscle chains and tendons, thus adding to the snake's flexibility. The intercostal and hypaxial muscles not only help in locomotion but also in the passage of prey for digestion and in respiration.

Snakes have no distinct cervical region but the first two cervical vertebrae lack ribs. There is no sternum or costal cartilages so each rib pair attaches by muscles to the inner surface of the ventral scales. Post cloaca there are no distinct ribs but vertebral processes fork ventrally and dorsally to protect the lymph hearts (Figs. 5.13 and 5.16). The tail is always shorter than the trunk (Hoffstetter & Gasc 1970).

GENERAL INTEREST

The cobra has long curved ribs on its cervical vertebrae, which can be rotated outwards causing a fold of loose skin to spread. This hood is then inflated with air from the lungs.

Locomotion

Snake locomotion involves two kinetic types: undulating and sidewinding (Fig. 5.14). They often combine several methods of undulation according to the local terrain (Bellairs 1969a).

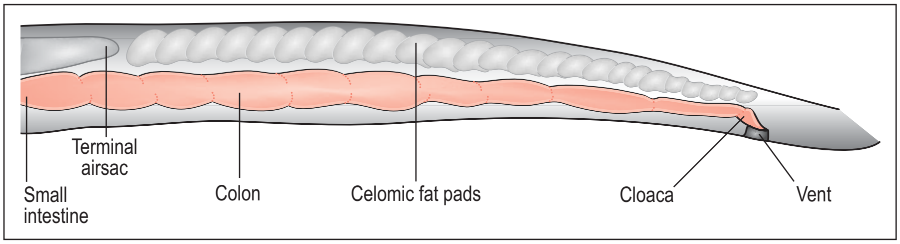


Figure 5.6 • Internal anatomy of caudal third showing colon.

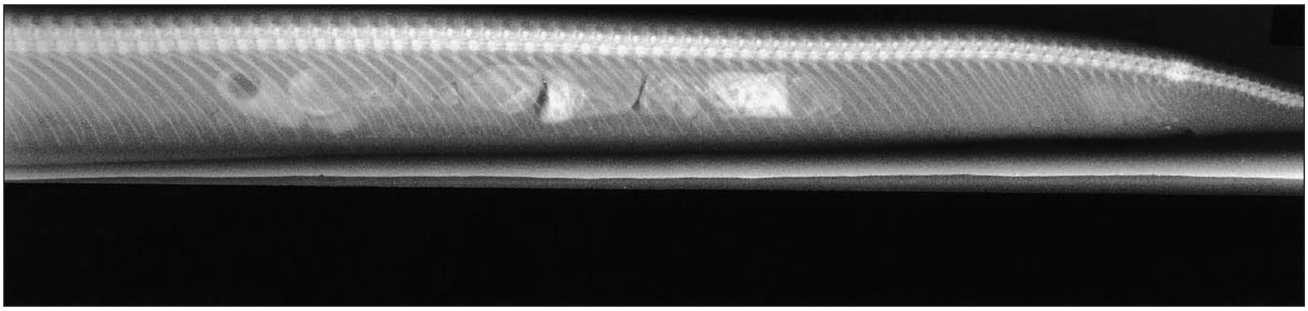


Figure 5.7 • Radiograph of caudal third of the snake. Other viscera are not visible radiographically as they merge with the large celomic fat pads in this area. Note the absence of ribs post cloaca.

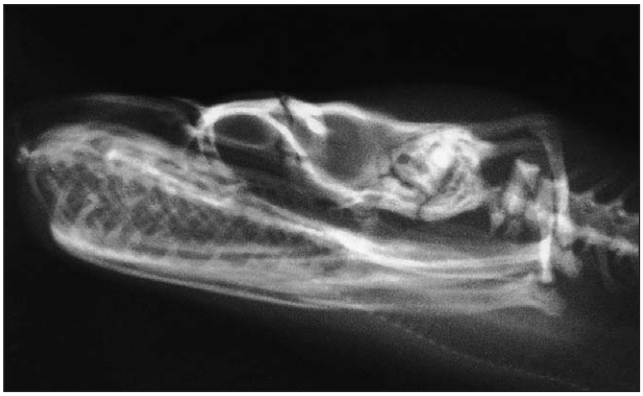


Figure 5.8 • Lateral radiograph of skull of common boa (*Boa constrictor*) showing flexible serpentine skull. Note heavily ossified braincase, backwardly pointing teeth and mobile quadrate bone.

Lateral undulation

This is when the snake wriggles laterally. When the body comes in contact with an object or rough surface it thrusts itself forward. As they need a minimum of three contact points, snakes would have difficulty advancing on very smooth surfaces like glass. Long, thin snakes like racers can move faster because they can make more curves and more thrust. During swimming snakes use this movement, pushing against the resistance of the water (Pough et al. 2002).

Rectilinear

Rectilinear locomotion is where a snake moves forward in a straight line on its ribs, causing a wave effect. This method of motion is used by thick-bodied snakes like boas and pythons and is less conspicuous than other forms. It is also used for stalking prey. The ventral scales are loosely attached and linked to the ribs by segmental muscles. Contraction of these muscles helps to draw the snake forward (Pough et al. 2002).

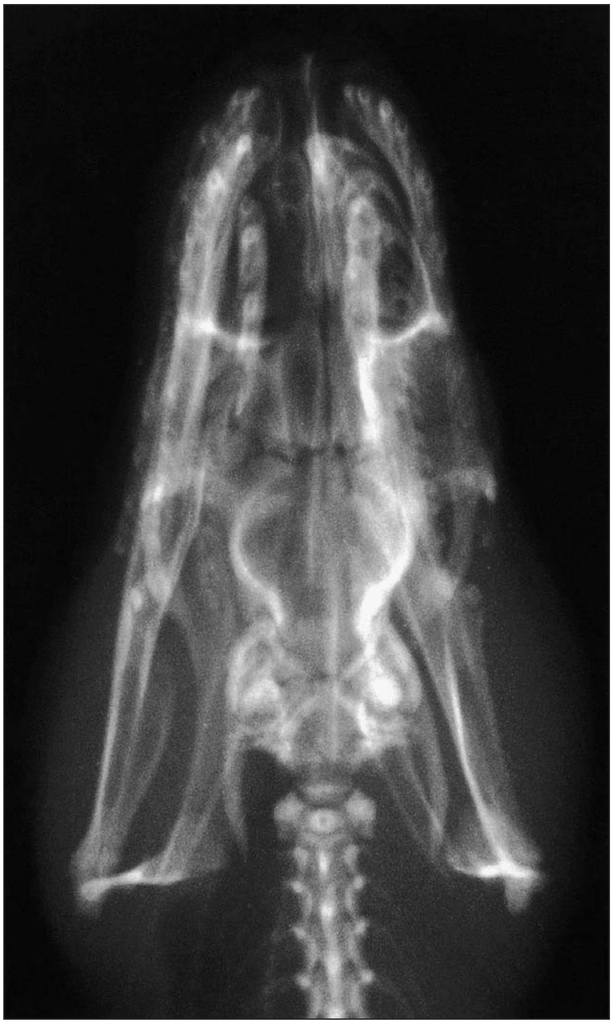


Figure 5.9 • Dorsoventral radiographs of above demonstrating lack of mandibular symphysis.

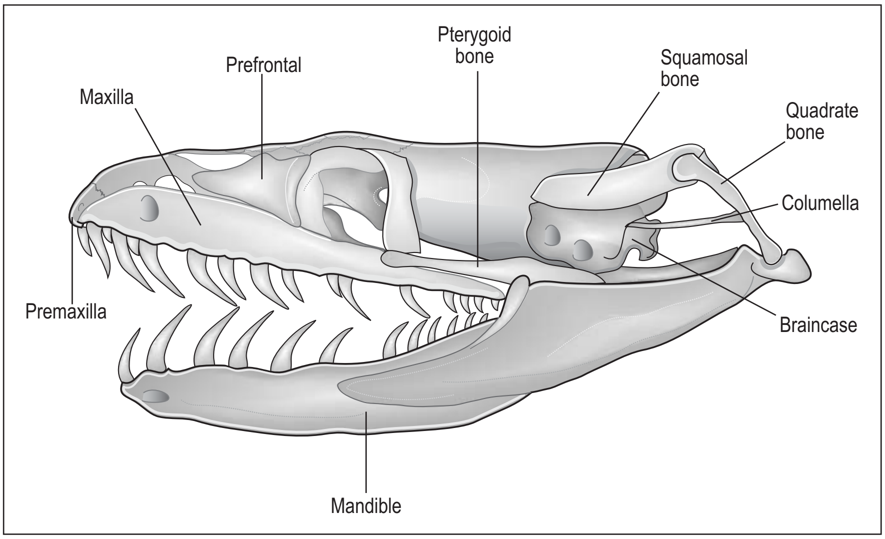


Figure 5.10 • Skull of simple snake.

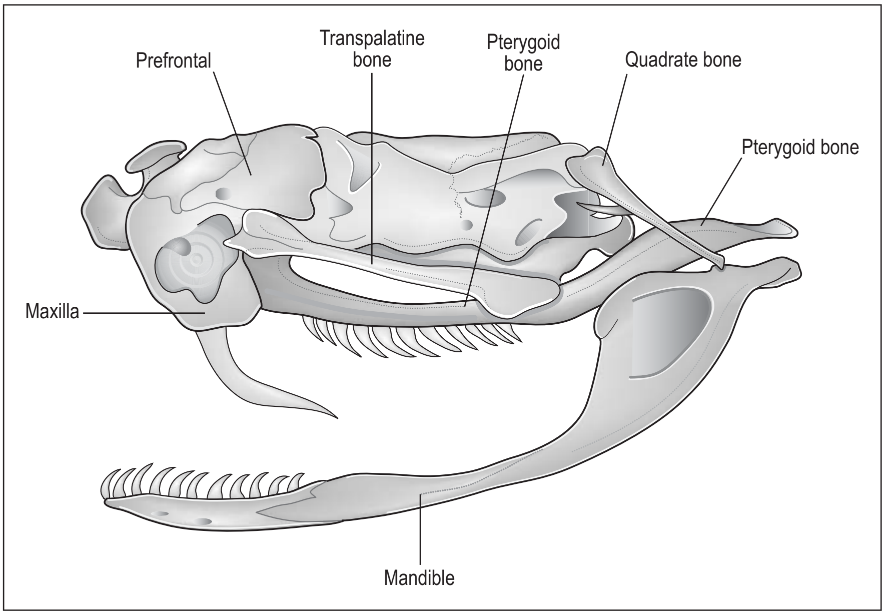


Figure 5.11 • Advanced snake skull as seen in vipers demonstrating the shortened maxilla. The prefrontal bone can be raised like a hinge to rotate the front fangs for striking.

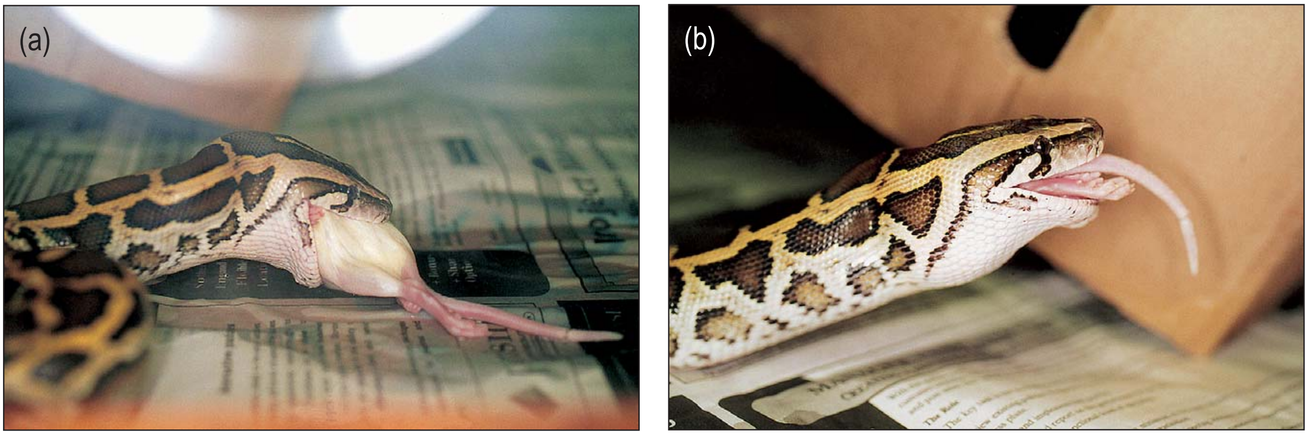


Figure 5.12(a&b) • Burmese python (*Python molurus*) eating a rat. The snake's skull is modified to allow an animal with a small head to consume prey large enough to sustain their length. The tooth-bearing bones of the skull are able to move independently of each other, allowing the snake to "walk" its jaw over large prey.

Concertina

The concertina method is used mainly by burrowing snakes. This is where the snake bunches a few s-shaped loops against the body wall and then straightens out at the front to move forward (Pough et al. 2002).

Sidewinding

Sidewinding is a specialized locomotion devised by snakes such as rattlesnakes and vipers that live in deserts. It involves throwing the head forward while at the same time throwing a loop of body forward, leaving a characteristic 'J'-shape behind. The body actually moves at right angles to the direction the snake is travelling and is the fastest method of maneuvering through loose sand (Pough et al. 2002).

Spurs

With elongation, the snake has lost its pectoral girdle to facilitate the swallowing of large prey. Some of the more primitive Boidae have retained pelvic vestiges, "spurs", and these can be seen on either side of the vent (Figs. 5.15 and 5.16). These short bones are covered in keratin and articulate with a longer bone lying within the rib cage. An attached muscle serves to flex and extend the spurs, which are used during courtship and mating (Evans 1986).

CARDIOVASCULAR SYSTEM

Snakes have a 3-chambered heart with a complete atrial separation and just one ventricle. It is long and slender and lies just cranioventral to the bifurcation of the trachea,

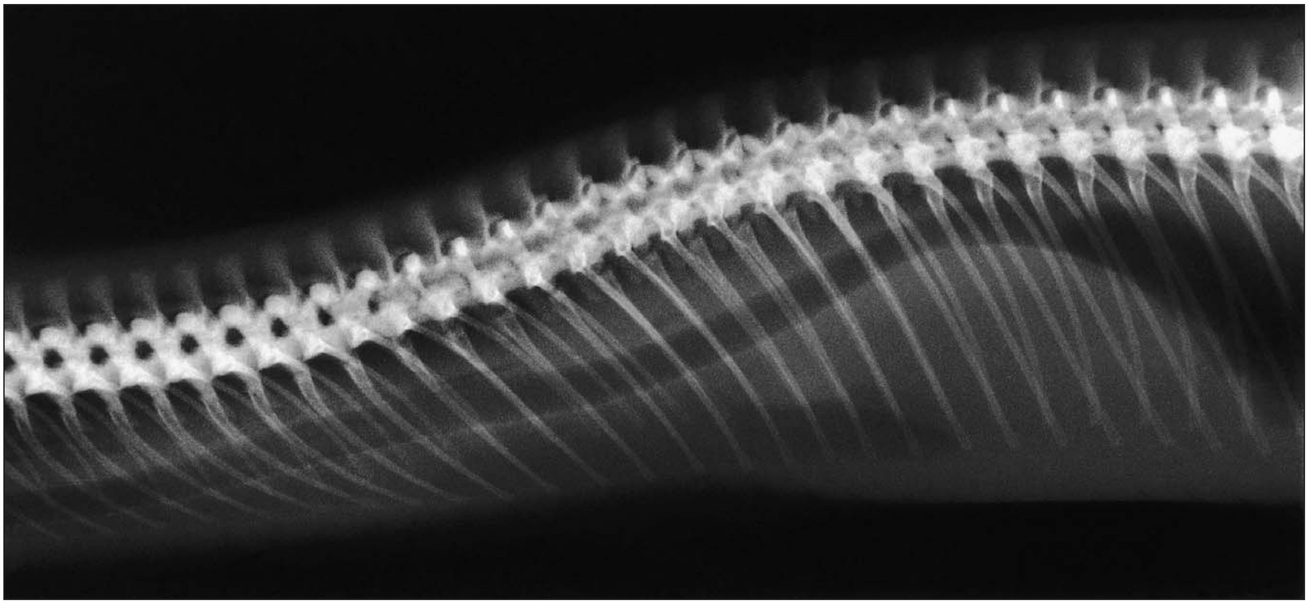


Figure 5.13 • Radiograph of vertebrae and ribs which extend the length of the body to the vent. Post cloacally the vertebral processes are forked to protect the lymph hearts. Note the precardial fat pad.

KEY POINTS

Anatomical adaptations for locomotion:

- Up to 400 flexible vertebrae
- Ribs that extend to midline from atlas to vent
- Large interconnecting muscle bundles
- Ventral gastropeges linked by pleated membranes
- Elastic dermis and loose skin

CLINICAL NOTE

Avoid the ventral approach when operating so as to avoid the ventral abdominal vein. When doing a celiotomy the incision is made between the second and third dorsal row of lateral scales. This also preserves the ventral scales for locomotion and keeps the wound from getting soiled by the substrate (Funk 1996).

about a third of the way down the body. The heart is fairly mobile as there is no diaphragm to hold it in place, and this allows prey items to pass by it.

Paired right and left aorta fuse caudal to the heart to form the dorsal aorta. A large ventral abdominal vein lies along the inner surface of the midline and so this must be avoided when making a celiotomy incision. A renal portal system is present, as in all reptiles.

The carotid arteries are asymmetrically placed. The more advanced snakes like the colubrids and vipers have only the left carotid artery, the right one being rudimentary.

As is the case with other reptiles, lymphatic vessels are prominent. Dilations of the lymph vessels (lymph hearts) are found on each side of the tail base where they are protected by modified, forked caudal vertebrae.

Venepuncture sites

(See Redrobe & MacDonald 1999.)

- Ventral coccygeal vein – Insert the needle caudally to avoid the hemipenes in males.
- Cardiac puncture – This is usually recommended in species over 300 g in weight. The needle is inserted into the ventricular apex and the syringe allowed to fill passively according to the cardiac cycle. There is little danger of leakage post sampling due to the slow heart rate and low blood pressure (Murray 2000).
- Dorsal palatine vein – This can be easily visualized in medium to large sized snakes. It lies on the dorsal oral cavity, medial to the palatine row of teeth. Hematoma formation is common post sampling and saliva may contaminate blood samples (Murray 2000).
- Jugular cutdown – This is possible on collapsed or anesthetized animals.

RESPIRATORY SYSTEM

Upper respiratory tract

The glottis lies forward and is easily visualized making intubation for anesthesia very easy. It is very mobile and can be extended laterally while feeding to allow breathing while ingesting prey (Fig. 5.17). It lies against the choana dorsally when the mouth is closed. The trachea has incomplete car-

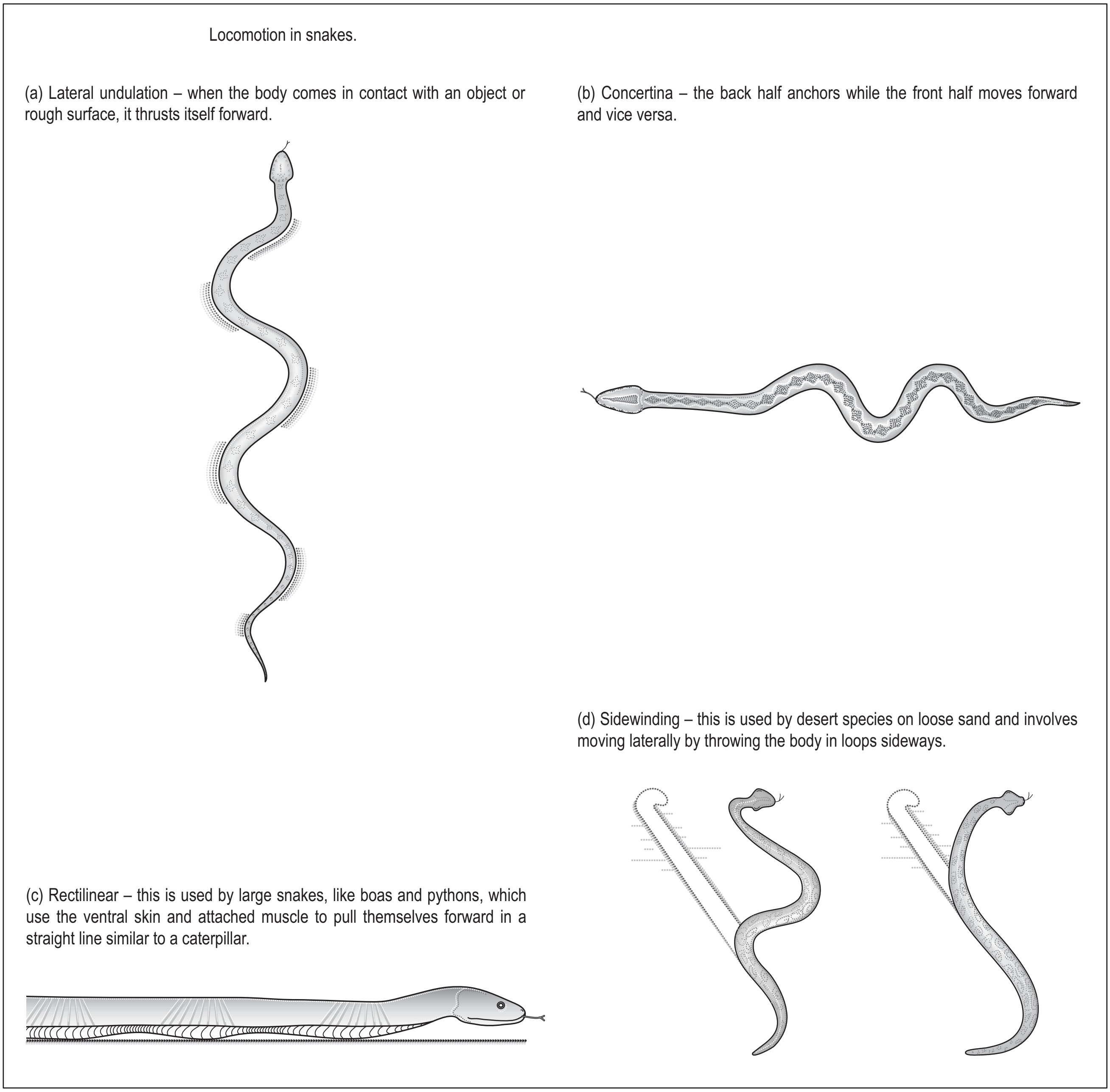

Locomotion in snakes.
(a) Lateral undulation – when the body comes in contact with an object or rough surface, it thrusts itself forward.
(b) Concertina – the back half anchors while the front half moves forward and vice versa.
(c) Rectilinear – this is used by large snakes, like boas and pythons, which use the ventral skin and attached muscle to pull themselves forward in a straight line similar to a caterpillar.
(d) Sidewinding – this is used by desert species on loose sand and involves moving laterally by throwing the body in loops sideways.

Figure 5.14 • Locomotion in snakes.
(a) Lateral undulation – when the body comes in contact with an object or rough surface it thrusts itself forward
(b) Concertina – the back half anchors while the front half moves forward and vice versa
(c) Rectilinear – This is used by large snakes, like boas and pythons, which use the ventral skin and attached muscle to pull themselves forward in a straight line similar to a caterpillar
(d) Sidewinding – this is used by desert species on loose sand and involves moving laterally by throwing the body in loops sideways

tilaginous rings, with rigid cartilage ventrally and the dorsal fourth being membranous (Funk 1996). Like all reptiles, snakes have a poorly developed mucociliary apparatus and rely on body positioning to help clear mucus and inflammatory exudates. They have no vocal cords but hiss by forcing air through the glottis – the pitch will depend on the width of the aperture and the loudest noise is made during expiration (Bellairs 1969d; Liem et al. 2001b).

CLINICAL NOTE

Snakes have no effective cough reflex so it is possible for experienced handlers to intubate a conscious animal and induce anesthesia by isofluorane. However, this inability to cough up exudates make the snake very susceptible to pneumonia.

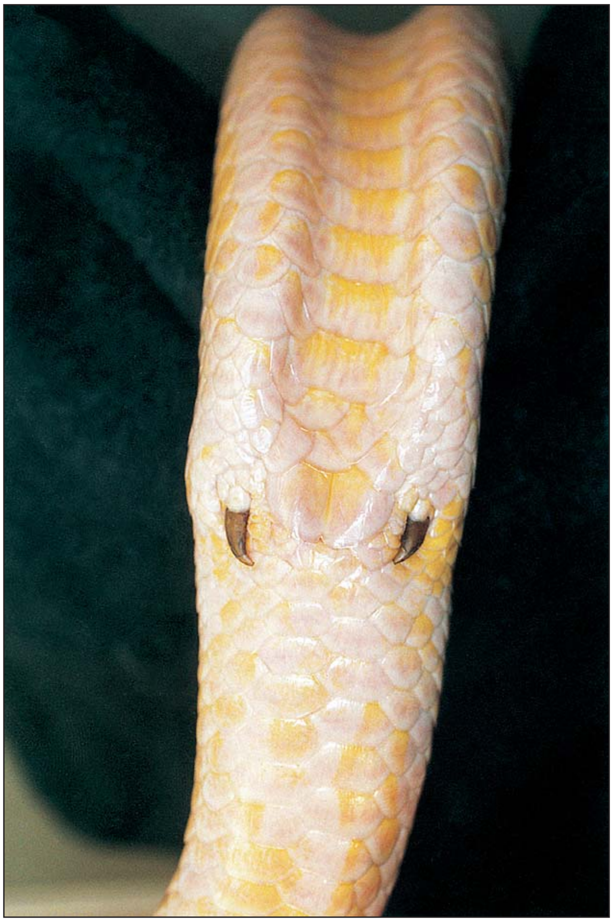


Figure 5.15 • Albino male Burmese python (*Python molorus*) showing vestigial spurs.

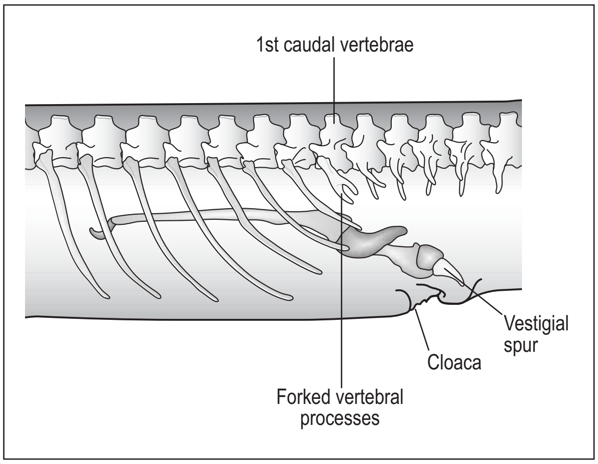


Figure 5.16 • Vestigial pelvic girdle and spurs in a python.

Lower respiratory tract

In keeping with body elongation many snakes have evolved one functional lung. The viperids have only one lung; the colubrids have one functional lung (the left lung is vestigial) and the more primitive boids have two saccular lungs, although the right lung is slightly longer (Evans 1986; McCracken 1999). The right lung extends from the heart to just cranial to the right kidney (Figs. 5.1 and 5.4).

Structurally, the cranial lung is simple and unicameral (single chambered), with a good blood supply, and performs the air exchange. Like in the Scincidae lizards, the caudal third is non-respiratory and functions like an airsac (Perry 1989). Aquatic snakes have an airsac that extends caudally to the cloaca and acts as a buoyancy aid (Bellairs 1969d).

In some snakes the vascular portion of the lungs extends into the dorsal trachea, creating a saccular extension to the tracheal rings that is capable of gaseous exchange (McCracken 1999).

CLINICAL NOTE

Snakes have a very fragile lung so perform intermittent positive-pressure ventilation (IPPV) with care, so as to avoid lung rupture.

The respiratory cycle

Respiration is controlled by the dorsal and ventrolateral sheet of intercostal muscles, which extend along almost the entire length of the trunk. Some snakes also use the avascular airsac like bellows in order to ventilate the lungs when the passage of food compresses them. In snakes inspiration is both passive and active. Relaxation of the expiratory muscles

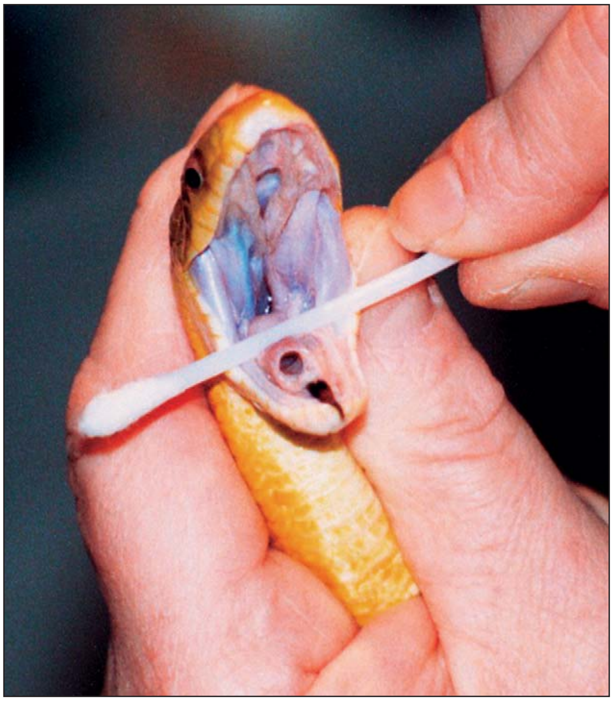


Figure 5.17 • Open mouth of Rat snake (*Elaphe obsoleta*) showing open glottis. In snakes the trachea is very mobile and can be extended out of the mouth to allow breathing while swallowing large prey. (Photo by Janet Saad)

starts the passive part of inspiration. The intercostal muscles then contract, decreasing intrapulmonary pressure and resulting in active inspiration. Passive expiration then occurs as these muscles relax and the lung recoils (Wood & Lenfant 1976).

DIGESTIVE SYSTEM

All snakes are carnivorous so the gastrointestinal tract is a relatively simple, linear duct, which extends from the oral cavity to the cloaca (Fig. 5.1).

Dentition

Snakes swallow their prey whole without mastication so the teeth function solely in food prehension. Consequently, they are long, thin and backwardly curved to prevent the escape of prey. All snakes have pleurodont teeth that are attached to the medial jawbone and are continually being replaced by new teeth lying in reserve in the gums (Fig. 5.18). Each tooth lasts only a few months before being shed and swallowed with the prey. In venomous species some maxillary teeth are modified into fangs (Edmund 1970).

The number of teeth varies between species but most snakes seen in veterinary practice have six rows of teeth in total: one row on each lower jaw and two rows on each maxillary and palatine or pterygoid bones of the upper jaw (Edmund 1970) (Figs. 5.19 and 5.20). Copious amounts of saliva are produced from the palatine, lingual, sublingual and labial salivary glands during swallowing, which moistens and lubricates the prey.

Venom glands

These are modified labial salivary glands, that produce venom that immobilize the prey preventing damage to the delicate skull. The venom contains collagenases, phospholipases, proteases and injection into the prey is under voluntary control (Bellairs 1969c).

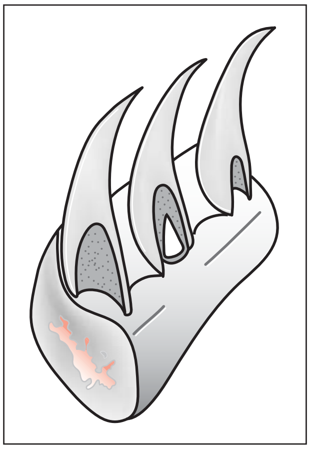


Figure 5.18 • All snakes have pleurodont teeth. These are thin and backwardly pointing to prevent escape of prey.

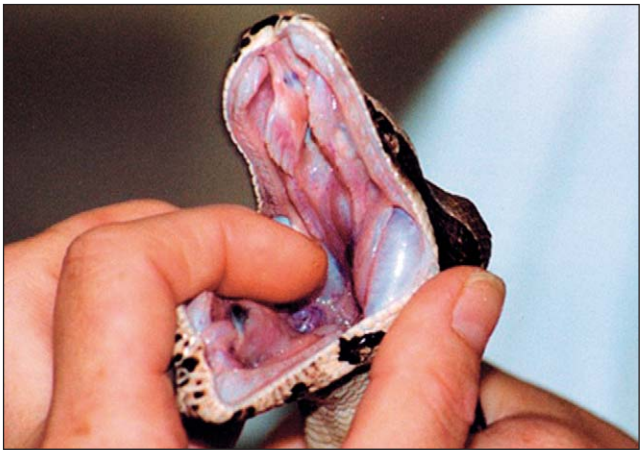


Figure 5.19 • Ventral view of maxillary arcade. Most species seen in practice have four rows of upper teeth. (Photo by Janet Saad)

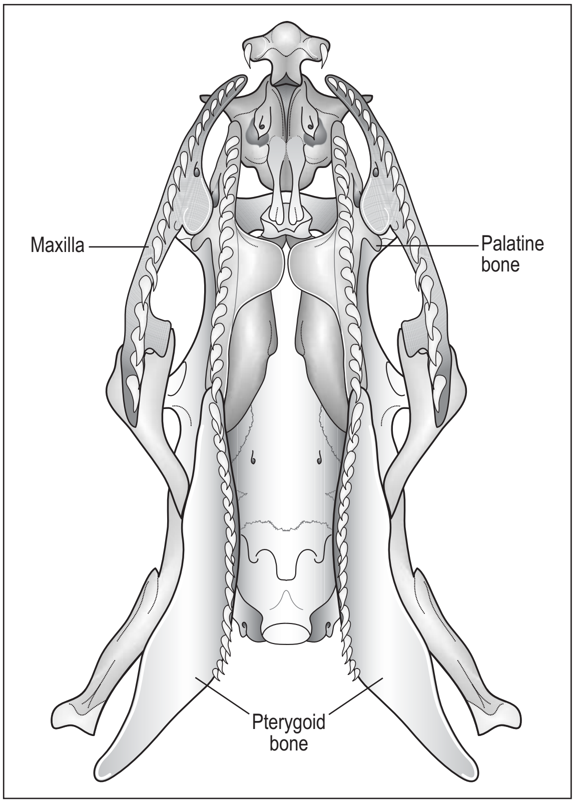


Figure 5.20 • Ventral view of maxilla showing maxillary and palatine/pterygoid dental arcades.

Rear-fanged (opisthoglyphous) snakes

In about one third of the colubrids the caudal labial gland becomes modified into a distinct capsular gland lying behind the eye and just above the lips. This gland is known as Duvernoy's gland and its function is to secrete venom to immobilize prey. Venom passes from this gland into a modified tooth at the caudal maxilla. These *rear fangs* are grooved and able to inject venom into prey. Like all teeth the fangs are shed regularly to be replaced by the reserve fangs (Bellairs 1969c; Evans 1986; Pough 1998a, 1998b).

In general the back-fanged snakes are not so venomous, the exception being the Boomslang (*Dispholidus typus*), which can cause fatalities (Fig. 5.21). The main aim of the venom is actually to incapacitate the prey so that it cannot damage the mouth while being eaten.

Front-fanged snakes

In these snakes the venom gland is large, separate from the labial glands, and lies behind the eye. A single long duct runs rostrally into fangs situated at the rostral maxilla. Some cobras can actually spit venom over 2 m away. In Elapidae the fangs remain erect and cannot fold (*proteroglyphous*) (Pough et al. 2002).

Viperidae have even more highly modified fangs (*solenoglyphous*). They are so long that when the mouth is closed the fangs lie folded backwards in a sheath along the roof of the mouth in an area of no teeth (*diastema*). The shortened maxilla is hinged and mobile. When the mouth opens the pterygoid muscles contract, pulling up the palatopterygoid so that the fangs are raised for striking (Pough et al. 2002) (Fig. 5.22).

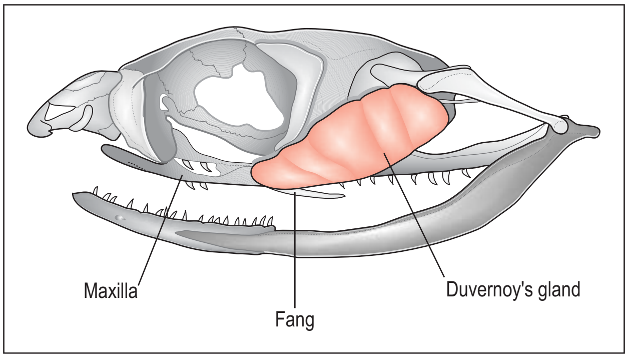


Figure 5.21 • Rear fangs – Boomslang (*Dispholidus typus*) showing location of Duvernoy's gland and position of rear-grooved fangs.

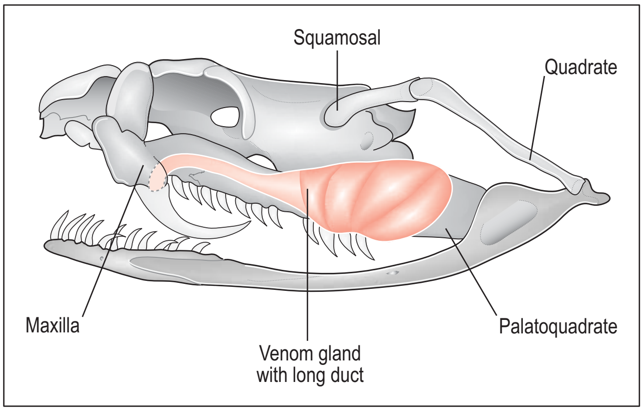


Figure 5.22 • Front fangs – Rattlesnake (*Crotalus* sp.) showing location of venom gland with duct opening into grooved front fangs. The fangs are folded but the hinged maxilla can be raised to erect fangs for striking.

Tongue

The tongue is long, slender and forked and lies in a sheath beneath the glottis and rostral trachea (Fig. 5.23). It is very mobile and can be protruded through the lingual notch or fossa without the snake opening its mouth. It functions in olfaction, taste and touch (Fig. 5.24).

Gastrointestinal tract

The esophagus is relatively thin walled and amuscular as the axial musculature plays a major role in the transportation of

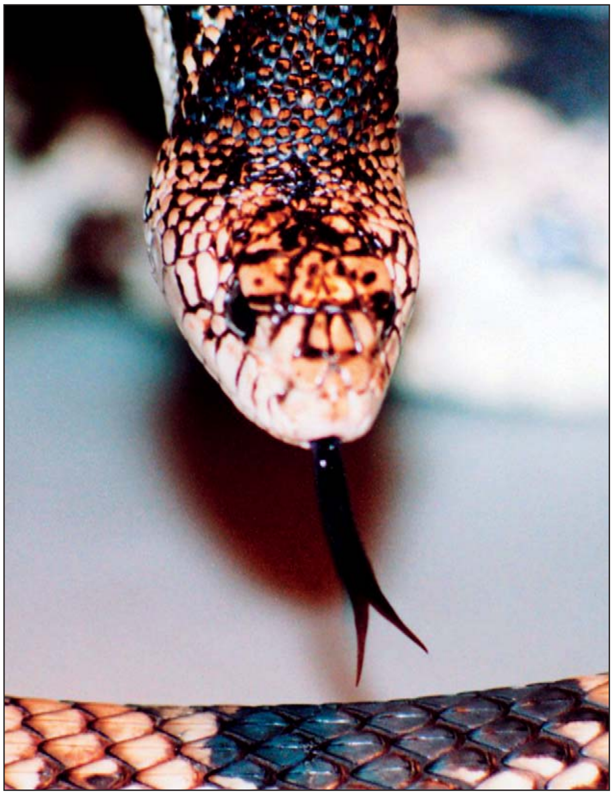


Figure 5.23 • Forked tongue of snake. (Photo by Janet Saad)

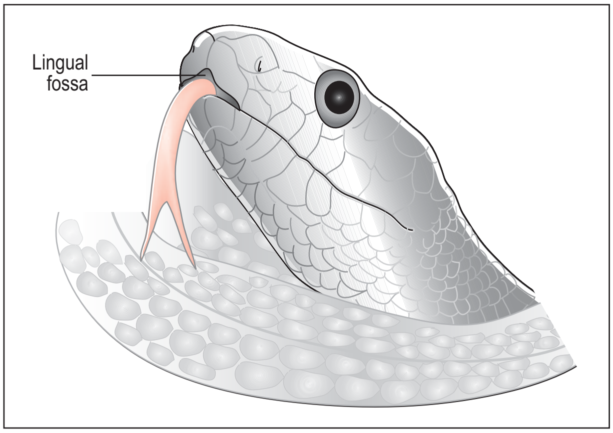


Figure 5.24 • The tongue is very mobile and can be protruded through the lingual fossa without the snake opening its mouth.

food to the stomach. It is highly distensible to allow for prey, which may remain alive there for many hours. Often the only distinguishing feature between the stomach and esophagus is that the stomach has a more glandular mucosa. The stomach is fusiform and there is no well-defined cardiac sphincter, causing easy regurgitation of food (Figs. 5.1 and 5.4).

The esophagus also plays a role in food storage because the stomach is relatively small and may not be able to accommodate the entire prey (particularly with cannibalistic species which often consume prey as long as themselves). Digestion begins as soon as even part of the prey reaches the stomach and is a rapid process. Absorption however is very slow. As the whole prey is utilized, including the skeleton, it may take up to 5 days for a large snake to digest a rat. Only the keratinous structures like fur are finally excreted as an undigested pad called the felt (Fig. 5.25).

GENERAL INTEREST

In egg-eating snakes (*Dasypeltis* spp.) the cranial esophagus is closely attached to the first 30 or so presacral vertebrae. These vertebrae have modified ventral spines against which the shell is crushed by longitudinal bands of muscle. The egg contents are expelled into the stomach while the broken shell is regurgitated up the esophagus.

CLINICAL NOTE

When stomach-tubing snakes, infuse slowly and hold them vertically for 30 seconds post feeding to prevent regurgitation through the weak cardiac sphincter.

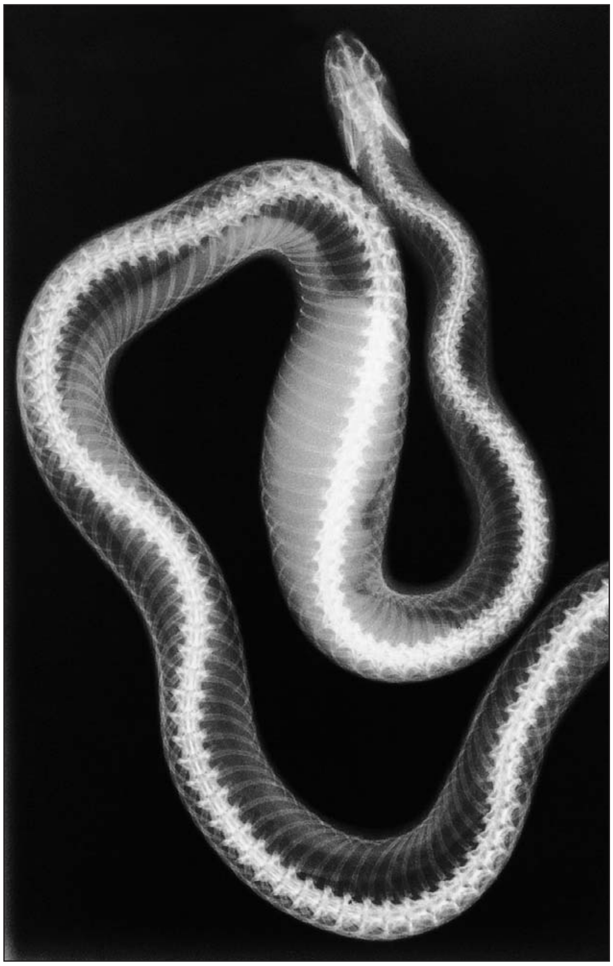


Figure 5.25 • Bull snake with esophageal and gastric impaction after the owner changed the diet from mice to rats. The combination of lack of humidity and increased size and fur length of prey contributed to a fatal impaction.

The liver is elongated and may be divided into two to three separate lobes. As snakes consume large meals infrequently a gall bladder is essential to help digest fat. The pancreas is ovoid and found caudal to the gall bladder on the mesenteric border of the duodenum (Fig. 5.1). In some species the spleen is adherent to the pancreas, creating the splenopancreas. The small intestine is fairly straight and a cecum is present is some Boidae species.

The large intestine is separated from the cloaca by a distinct fold. Paired fat bodies, which are often vascularized, lie in the caudal celomic cavity. In snakes the cloaca is linear rather than round and is divided into three sections by mucosal folds. Cloacal scent glands are present in some snakes and serve as a warning mechanism by producing foul smelling secretions (Evans 1986).

URINARY SYSTEM

The paired kidneys are located in the dorsocaudal abdomen with the right kidney being more cranial than the left (Figs. 5.1 and 5.26). They are brown in color, elongated, have about 25–30 lobes, and stretch for 10 to 15 percent of the total snout-to-vent length (Bellairs 1969d). The ureters are elongated, with the right longer than the left, and enter the cloaca dorsally where they are distinct from the vas deferens or oviduct. In some species they may dilate slightly at distal end to form a small urinary reservoir. There is no bladder (Fox 1977).

Male snakes have a sexual segment to the kidney. This provides a secretion rich in protein and lipids, which is used as a copulatory plug. This plug blocks the terminal oviduct for 2–4 days after copulation.

REPRODUCTIVE SYSTEM

Sexual maturity

Smaller species can reach sexual maturity in one year but larger, more long-lived species, may not be sexually mature until 5 years of age.

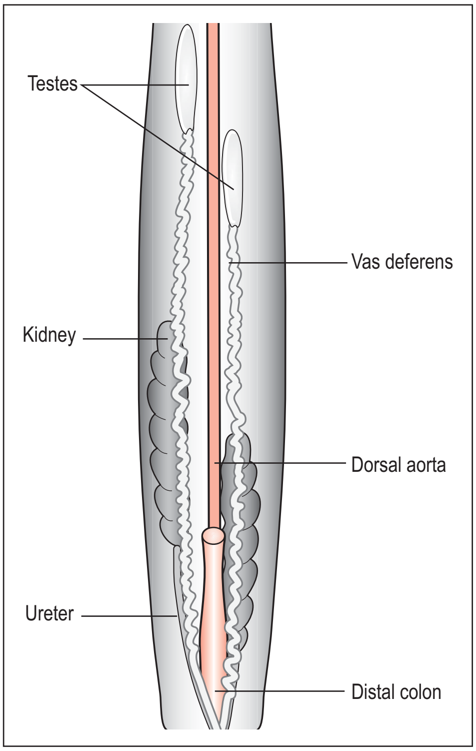


Figure 5.26 • Urogenital system of male snake (celomic fat bodies have been removed).

SEXUAL DETERMINATION

Snakes can show some sexual dimorphism, such as difference in size, but in general the signs are subtle. A number of methods are therefore used to sex snakes:

- Counting the number of subcaudal scales – The males have longer tails than females (Boidae).
- Measuring the tail base – The male tends to be broader due to the presence of hemipenes.
- Measuring the spurs – Vestigial spurs are bigger in the male (Boidae).
- Probing – In the male a probe can be inserted for about 6–10 subcaudal scales while in the female it is only 2–3 scales (Fig. 5.27).
- Everting the hemipenes – This can be done by gently squeezing the tail base or injecting saline.

Breeding season

In the wild, the breeding season is in spring in temperate and subtropical climes, after hibernation. In tropical regions the start of the wet season provides an ideal climate for egg incubation.

Male

The testes are intra-abdominal and situated between the pancreas and the kidneys. Male snakes have two hemipenes, which are paired, saclike caudal extensions of the cloaca and lie within the ventral tail base (Fig. 2.11). Each hemipenis has a retractor muscle that extends from the tail vertebrae to the tip and sides of the hemipene and large anal glands lie above the hemipenes. The hemipene, retractor muscle, and anal gland are all surrounded by the larger propulsor muscle. When the hemipene becomes engorged with blood the muscle contracts to evert it out like a finger from a glove. After engorgement has subsided the retractor muscle then works to retract and invert the hemipene (Bellairs 1969g; Evans 1986; Funk 1996) (Fig. 2.11).

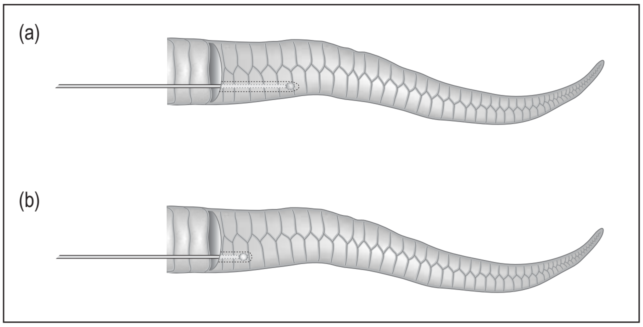


Figure 5.27 • The sex of a snake can be identified by gentle probing distal to the cloaca.
(a) A depth of over six subcaudal scales may be reached if the snake is male.
(b) A depth of less than two to three scales will indicate it is female.

Female

The ovaries are paired and located asymmetrically near the pancreas. The right ovary is usually larger and more cranial than the left. The left may be reduced or undeveloped. Snakes can be oviparous or viviparous (Palmer et al. 1997; Pough 1998a).

Maternal behavior

Some female Indian pythons (e.g., *Python molorus*) can generate a 7° C increase in heat by spasmodic contraction of the muscles as they coil around their eggs. This method is unique among reptiles and is facilitated by their large body size and the way they prevent heat loss by coiling tightly around the egg mass. Unlike mammalian shivering the muscles contractions are coordinated. At the same temperature the metabolic rate will be 20 times that of a non-brooding snake (Bartholomew 1982; Bennett & Dawson 1976).

Copulation

The male initiates courtship by moving his body over the female and rubbing his tail against her. If the female is receptive she will dilate her cloaca and raise her tail. Copulation can last from 2 to 20 hours. During copulation one hemipene is evaginated and inserted into the cloaca of the female.

The hemipene has spines and ridges that enable it to remain for long periods in the cloaca. It is then withdrawn by the action of the retractor muscle. During multiple matings the male can use the right and left hemipene alternately.

Sperm storage

Some female snakes can store sperm in a cavity lined by mucosa glands near the top of the oviduct where it is kept until conditions are right. This can be stored for months or even years and explains why a snake may suddenly appear fertile in the absence of a male (Bellairs 1969g).

SENSES

Sight

Sight is quite poor in snakes as they may have evolved from burrowing snakes. The snake eye is very different to that in lizards and chelonians as it is small with a relatively large cornea and has no scleral ossicles. The eyeball is spherical and lined by a fibrous sclera. The eyes have no eyelids but have fused to form a protective *spectacle* or *brille* over the cornea (Fig. 5.28). The Harderian and lacrimal glands secrete into the subspectacular space, which is then drained by the nasolacrimal duct. Infections here can lead to bullous spectaculopathy and subspectacular abscesses where the fluid cannot drain away. There is no nictitating membrane. Unlike lizards, eye mobility beneath the spectacle is very limited (Underwood 1970).

Most reptiles focus the eye by using muscles in the ciliary body to change the lens curvature. However, snakes have a reduced ciliary body, relying on movement of the iris muscles instead, and as a consequence the lens is spherical in shape and accommodation is poor. The pupil shape varies with the mode of life and the habitat in which the snake lives and may be round, elliptical, or even horizontal in some arboreal species (Bellairs 1969f; Pough 1998a; Underwood 1970).

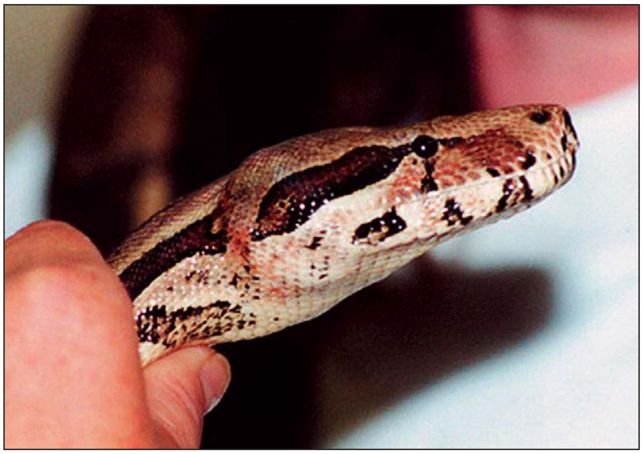


Figure 5.28 • The snake has no eyelids. Instead they are fused to form the transparent spectacle or brille which is shed with the other scales during ecdysis. (Photo by Janet Saad)

Unlike lizards, snakes have both cones and rods in their retina, although many diurnal forms have lost their rods. Only a few snakes have a conus papillaris (similar to the avian pecten) arising from the optic nerve papilla.

Hearing

Snakes have no external aural structures, no tympanic membrane, and only a narrow tympanic cavity (Murray 1996). The columella (stapes) is directly attached to the quadrate bone and the inner ear appears to be well developed and sensitive to ground vibrations. Contrary to popular belief, snakes are not deaf but hearing sensitivity is only over a limited low frequency in the range of 150–600 Hz. Snakes hear by literally having “an ear to the ground”. They pick up sensitive vibrations via the quadrate bone (which acts like an eardrum) and direct them to the inner ear and brain. Snakes do not vocalize between themselves but hiss or rattle as warning signals (Baird 1970; Bellairs 1969f).

Olfaction

This is the most developed of senses in snakes. Apart from the usual olfactory epithelium in the nostrils, snakes possess a highly developed *Jacobson's organ* (Fig. 2.14). This is a pair of domed cavities or vomeronasal pits lined with sensitive epithelium. The forked tongue is flicked out through a groove in the mouth called the lingual notch or fossa where it picks up scent particles from its surroundings. It then inserts the fork in the vomeronasal pits and sends information via the olfactory nerves to the brain (Bellairs 1969f; Parsons 1970).

Touch and taste

The tongue is an organ of taste, touch and smell. It lies in a sheath beneath the glottis and is protruded through the lingual notch or fossa, enabling the snake to protrude its tongue without opening its mouth. It is primarily a sensory organ that brings odor from the environment to the vomeronasal organ. Snakes in unfamiliar surroundings will flick their tongue in and out as they explore.

Heat sensing: the sixth sense

Some snakes possess specialized infrared receptors, or pits, which enable them to sense warm-blooded prey and strike to catch them, even in total darkness. They are located between the nostril and eye on the side of the head in pit vipers. Boas and pythons have a series of smaller, less sensitive slit-like openings on the upper and lower labial scales but the pattern and number varies between species. The pits are richly innervated via the ophthalmic, mandibular, and maxillary branches of the trigeminal nerve. They are so sensitive they can detect a temperature variation of as little as 0.003° C (Barrett 1970). These thermal cues combine with visual cues to give the snake a general image of its surroundings (Bellairs 1969f; Bennett 1996).

INTEGUMENT

The scales are formed by thickened parts of epidermis between which are foldings of thin skin, and this allows for great expansion when a snake consumes its prey (Fig. 5.29). The *gastropeges* are larger and thicker to provide support. The subcaudal scales covering the ventral tail are usually paired. Snakes have few skin glands apart for the cloacal glands.

CLINICAL NOTE

Reptile skin is very inelastic so incising between the scales will improve flexibility.

Ecdysis

The snake grows by shedding their skin. Lymph fluid builds up between the old and new epidermal layers, causing the markings to become obscure and giving a blue appearance to the skin and spectacle. Snakes cannot see clearly around this time so may become more irritable than usual. Just before the shed takes place the spectacle clears and the skin circulation then becomes engorged, stretching the old skin and causing it to split. The snakes become more restless and start to crawl about and rub against rough surfaces. In healthy snakes the skin is shed in one piece from snout to tail and is generally 20% longer than the original (Fig. 5.30). It is colorless because the pigment cells are in the dermal layer.

Once ecdysis is completed the old inner layer becomes the new outer layer and gives the snake a wonderful luster and sheen. After shedding the snake may defecate and be very thirsty. Failure to eat may occur if the spectacles fail to shed, thus inhibiting vision (Fig. 5.31).

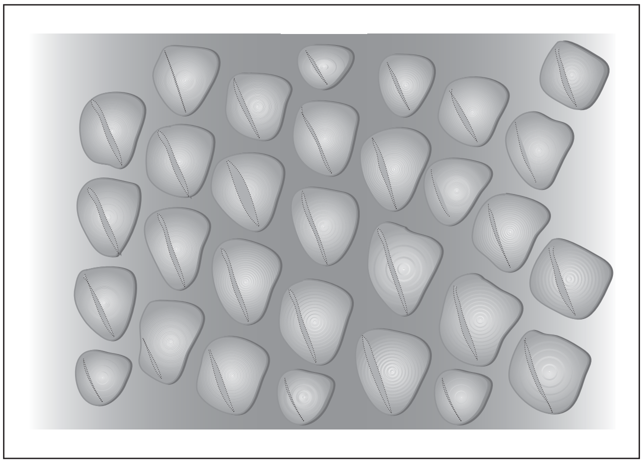


Figure 5.29 • Stretched snake skin showing the thin skin (alpha keratin) hinged in between the thick scales (beta keratin).

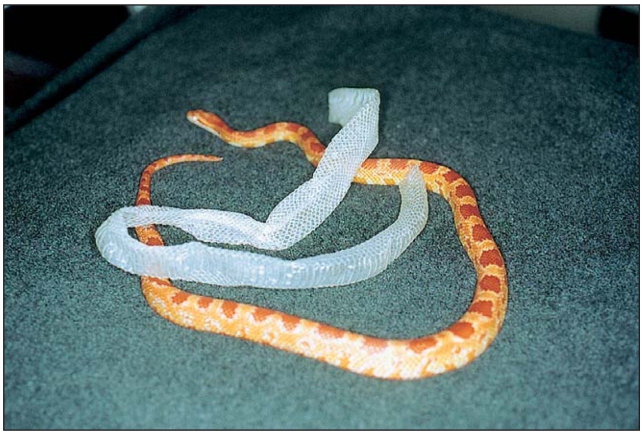


Figure 5.30 • Normal shedding.

CLINICAL NOTE

Failure to shed can be caused by lack of humidity in the vivarium. Increasing the humidity and providing rocks or logs for the snake to rub against will prevent dysecdysis. Warm water soaks and artificial tears can also literally help the “scales fall from the eyes” so that the snake can then see to eat.

GENERAL INTEREST

The Rattlesnake’s rattle is made from previous skin sheds left behind on the tail. Each time it sheds it leaves behind a horny segment on the tail. The sound is produced when the rattlesnake vibrates its tail, causing the segments to bang together (Bellairs 1969e; Evans 1986).

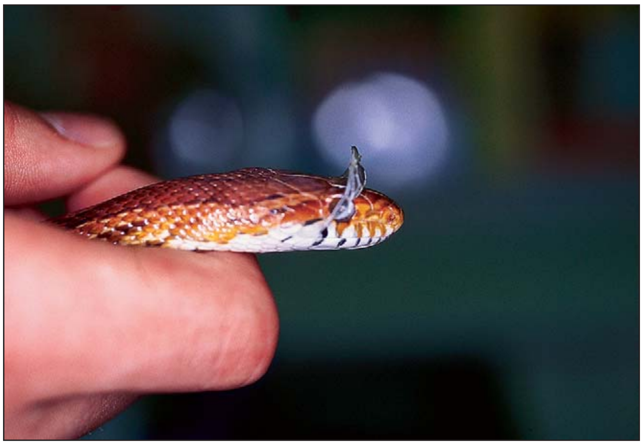


Figure 5.31 • Poor shedding or dysecdysis in a corn snake.

Frequency of shedding

The shedding frequency is affected by many factors, such as growth, season (e.g., post hibernation in spring), oviposition or parturition (8–10 days before these). Most snakes shed about 2 to 4 times a year.

REFERENCES

Baird, I. L. (1970) The anatomy of the reptilian ear. In C. Gans (ed.), *Biology of the reptilia*. Vol. 2, Morphology B. London: Academic Press. pp. 193–272.

Barrett, B. (1970) The pit organs of snakes. In C. Gans (ed.), *Biology of the reptilia*. Vol. 2, Morphology B. London: Academic Press. pp. 277–295.

Bartholomew, G. A. (1982) Physiological control of body temperature. In C. Gans & F. H. Pough (eds.), *Biology of the reptilia*. Vol. 12, Physiology C. London: Academic Press. pp. 167–204.

Bellairs, A. (1969a) *The life of reptiles*. Vol. 1. London: Weidenfeld and Nicolson. Body form, skeleton and locomotion; pp. 44–116.

Bellairs, A. (1969b) *The life of reptiles*. Vol. 1. London: Weidenfeld and Nicolson. Feeding and cranial mechanics; pp. 116–184.

Bellairs, A. (1969c) *The life of reptiles*. Vol. 1. London: Weidenfeld and Nicolson. The venom apparatus and venom; pp. 184–217.

Bellairs, A. (1969d) *The life of reptiles*. Vol. 1. London: Weidenfeld and Nicolson. The internal economy; pp. 217–282.

Bellairs, A. (1969e) *The life of reptiles*. Vol. 2. London: Weidenfeld and Nicolson. The skin; pp. 283–332.

Bellairs, A. (1969f) *The life of reptiles*. Vol. 2. London: Weidenfeld and Nicolson. Nervous system, psychology and sex organs; pp. 332–390.

Bellairs, A. (1969g) *The life of reptiles*. Vol. 2. London: Weidenfeld and Nicolson. Sex and reproduction; pp. 390–433.

Bellairs, A. (1969h) *The life of reptiles*. Vol 2. London: Weidenfeld and Nicolson. Growth, age and regeneration; pp. 458–488.

Bellairs, A. D., & Bryant, S.V. (1985) Autotomy and regeneration in reptiles. In C. Gans & F. Billett (eds.), *Biology of the Reptilia*. Vol. 15, Development B. New York: Wiley Interscience. pp. 302–350.

Bennett, A. F., & Dawson, W. R. (1976) Metabolism. In C. Gans & W. R. Dawson (eds.), *Biology of the reptilia*. Vol. 5, Physiology A. London: Academic Press. pp. 127–211.

Bennett, R. A. (1996) Neurology. In D. R. Mader (ed.), *Reptile medicine and surgery*. Philadelphia: WB Saunders. pp. 141–148.

Edmund, A. G. (1970) Dentition. In C. Gans (ed.), *Biology of the reptilia*. Vol. 1, Morphology A. London: Academic Press. pp. 117–194.

Evans, H. E. (1986) Reptiles – Introduction and anatomy. In M. E. Fowler (ed.), *Zoo and wild animal medicine*, 2nd edn. Philadelphia: WB Saunders. pp. 108–132.

Fox, H. (1977) The urogenital system of reptiles. In C. Gans & T. Parsons (eds.), *Biology of the reptilia*. Vol. 6, Morphology E. London: Academic Press. pp. 1–122.

Funk, R. S. (1996) Biology – snakes. In D. R. Mader (ed.), *Reptile medicine and surgery*. Philadelphia: WB Saunders. pp. 39–46.

Hoffstetter, R., & Gasc, J. P. (1970) Vertebrae and ribs of modern reptiles. In C. Gans (ed.), *Biology of the reptilia*. Vol. 1, Morphology A. London: Academic Press. pp. 201–302.

Liem, K. F., Bemis, W. E., Walker, W.F., & Grande, L. (eds.) (2001a) *Functional anatomy of the vertebrates*, 3rd edn. Fort Worth, Tex.: Harcourt College. The digestive system: Oral cavity and feeding mechanisms; pp. 532–556.

Liem, K. F., Bemis, W. E., Walker, W. F., Grande, L. (eds.) (2001b) *Functional anatomy of the Vertebrates*, 3rd edn. Fort Worth, Tex.: Harcourt College. Respiration; pp. 591–593.

McCracken, H. E. (1999) Organ location in snakes for diagnostic and surgical evaluation. In M. E. Fowler & R. E. Miller (eds.), *Zoo & wild animal medicine: Current therapy*, 4th edn. Philadelphia: WB Saunders. pp. 243–249.

Murray, M. J. (1996) Aural abscess. In D. R. Mader (ed.), *Reptile medicine and surgery*. Philadelphia: WB Saunders. pp. 349–352.

Murray, M. J. (2000) Reptilian blood sampling and artifact considerations. In A. Fudge (ed.), *Laboratory medicine – avian and exotic pets*. Philadelphia: WB Saunders. pp. 185–191.

Palmer, B., Uribe, M. C. et al. (1997) Reproductive anatomy and physiology. In L. Ackermann (ed.), *The biology, husbandry and healthcare of reptiles*. Vol. 1, The biology of reptiles. N.J.: TFH Publications. pp. 54–81.

Parsons, T. S. (1970) The nose and Jacobson's organs. In C. Gans (ed.), *Biology of the reptilia*. Vol. 2, Morphology B. London: Academic Press. pp. 99–185.

Perry, S. F. (1989) Structure and function of the reptilian respiratory system. In S. C. Wood (ed.), *Comparative pulmonary physiology – current concepts*. New York: Dekker. pp. 193–237.

Pough, F. H., Andrew, R. M., Cadle, J. E., et al. (1998a) *Herpetology*. Englewood Cliffs, N.J: Prentice Hall. Classification and diversity of extant reptiles; pp. 75–133.

Pough, F. H., Andrew, R. M., Cadle, J. E. et al. (1998b) *Herpetology*. Englewood Cliffs, N.J: Prentice Hall. Feeding; pp. 267–305.

Pough, F. H., Janis, C. M., & Heiser, J. B. (2002b) *Vertebrate life*, 6th edn. Englewood Cliffs, N.J: Prentice Hall. The lepidosaurs: Tuatara, lizards and snakes; pp. 294–341.

Redrobe, S., & MacDonald, J. (1999) Sample collection and clinical pathology of reptiles. In D. R. Reavill (ed.), *Clinical pathology and sample collection.* The Veterinary Clinics of North America: Exotic animal practice. Vol. 2. Philadelphia: WB Saunders. pp. 709–730.

Underwood, G. (1970) The eye. In C. Gans (ed.), *Biology of the Reptilia.* Vol. 2, Morphology B. London: Academic Press. pp. 1–93.

Wood, S. C., & Lenfant, C. J. (1976) Respiration: Mechanics, control and gas exchange. In C. Gans & W. R. Dawson (eds.), *Biology of the reptilia.* Vol. 5, Physiology A. London: Academic Press. pp. 225–267.

6

Avian anatomy and physiology

INTRODUCTION

The ability to fly has enabled birds to occupy a wide diversity of habitats and develop many adaptations for feeding. This has led to a large number of about 9700 extant species belonging to the class Aves, divided into about 27 avian orders. The largest order of all is the Passeriformes with over 5712 species and the smallest is the Struthioniformes with one species, the ostrich (King & McLelland 1984). Table 6.1 shows the types of bird most commonly seen in a veterinary clinic.

Birds evolved from reptiles and many similarities still remain. Like reptiles, birds have scales on their beak, legs and feet, a single occipital condyle, a single middle ear bone, the columella and a jawbone made up of five bones fused together (Quesenberry et al. 1997). They also have nucleated erythrocytes, a renal portal system and excrete uric acid (Maina 1996).

While reptiles and mammals show incredible diversity, the constraints of flight means the basic bird design varies very little from species to species. In fact there are fewer morphological variations among all bird species than among, for example, the mammalian order of Carnivora (with nearly 300 species) (Maina 1996). For this reason, this section will cover the anatomy and physiology of birds in general. The differences between the common orders can be seen in Table 6.6 at the end of the chapter.

Table 6.1 Common avian orders seen in veterinary practice

Order approx no	Species	Examples of species
Galliformes	214	Pheasants, domestic fowl, guinea fowl, quail
Anseriformes	161	Swans, geese, ducks
Psittaciformes	358	Cockatoos, budgies, cockatiels
Columbiformes	310	Pigeons, doves
Passeriformes	5712	Songbirds, canaries, zebra finches
Falconiformes	285	Eagles, hawks, falcons
Strigiformes	178	Owls, nightjars

Size range

In size, birds range from the hummingbird (*Trochilidae* spp.), which weighs 2 g, to the flightless ostrich (*Struthio camelus*) which can weigh up 120 kg. The largest flying birds weigh up to a maximum of 15 kg and range from the Mute swan (*Cygnus olor*) to the Andean condor (*Vultur gryphus*) (Kirkwood 1999).

Longevity

Birds tend to have longer life spans than mammals of similar size (Kirkwood 1999). Pigeons and swans can live for up to 30 years, while psittacines like African grays (*Psittacus erithacus*) and cockatoos (*Cacatua* spp.) commonly live for over 40 years. In the passerines the larger birds live longer than smaller ones: the raven can live for well over 40 years whereas canaries live from 8 to 16 years (Dorrestein 1997b).

METABOLISM

Birds are endothermic, meaning they have the ability to maintain a relatively stable body temperature, irrespective of the ambient temperature. At around 40° C (±1.5° C) birds' body temperature is about three degrees higher than mammals, so high metabolic rates are needed to maintain this and enable them to fly. Birds expend 20 to 30 times more energy than reptiles of similar body size so their circulatory and respiratory systems have evolved to rapidly provide energy and oxygen to cells (Dorrestein 1997a).

Passerine birds have the highest basal metabolic rate of all vertebrates, which is 50 to 60% higher than other birds of the same body size (Dorrestein 1997a; Maina 1996). During the day birds expend a lot of energy as they are constantly active with feeding, digestion, and flying. Many small birds can also store up fat reserves for energy overnight. Other small birds, like hummingbirds and swifts, can reduce metabolic rate to save energy and become torpid when the temperature

GENERAL INTEREST

Archaeopteryx – ancestor of all birds

Five remains of this earliest known bird have been found in late Jurassic limestone in Germany. The bird was bipedal, about the size of a magpie and still retained reptilian features like teeth, a long tail, claws on the wings, and simple ribs without uncinate processes. Distinctive avian features were the presence of feathers, paired clavicles, and a foot with opposing digits like present day passerines (Figs. 6.1 and 6.2). However Archaeopteryx must have been a poor flier as it had no carina or triosseal canal. This meant it had poorly developed pectoral muscles and must have relied on the deltoid muscle to lift the wing (King & King 1979; Maina 1996).

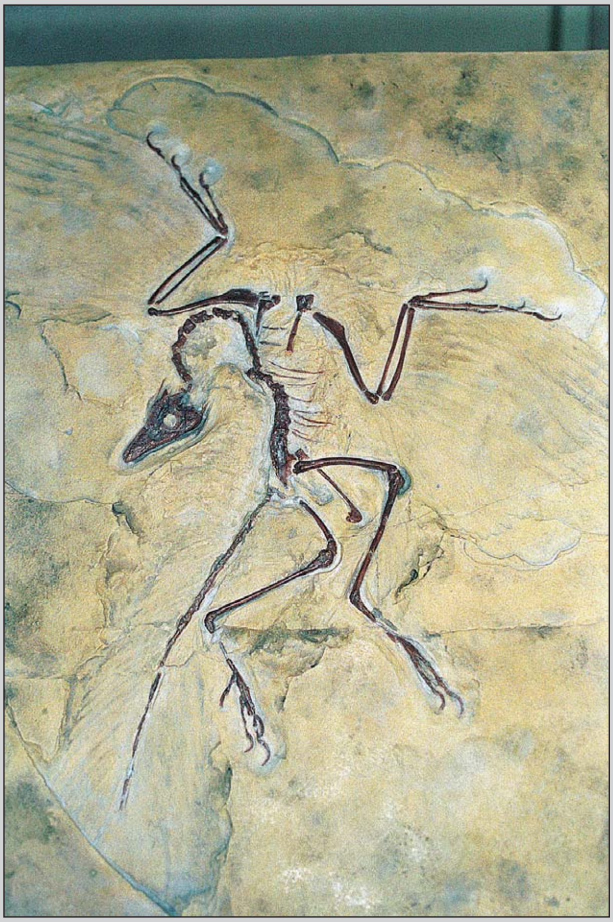


Figure 6.1 • Archaeopteryx lithograph. These fossils were found in late Jurassic marine deposits in southern Germany in the 1860s. They were so well preserved in the limestone that details of feathers (including the asymmetrical vane) could be identified, indicating their avian lineage.

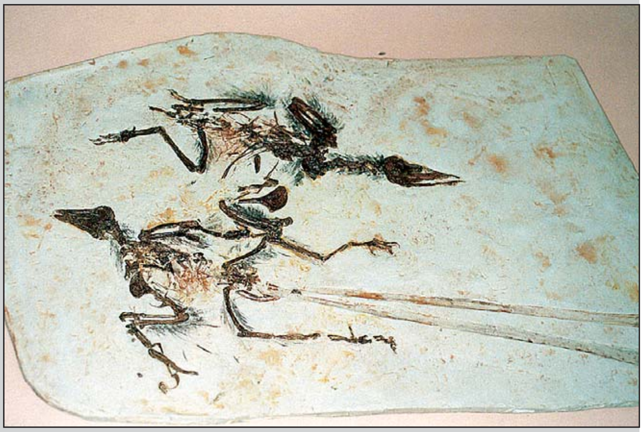


Figure 6.2 • Archaeopteryx.

drops. They warm out of this torpid state by shivering but this method is limited to small birds because the rate of rewarming is inversely related to the size of the bird and would just take too long in larger species (Blem 2000; Dawson & Whittow 2000; Dorrestein 1997a; Welty 1982b).

Birds have a rapid growth rate and reach full adult weight and size much faster than mammals of equal weight (Kirkwood 1999). Altricial birds growth faster than precocial ones. These rapid growth rates mean that there can be a three- or fourfold increase in energy requirements during growth (Blem 2000; Kirkwood 1999).

CLINICAL NOTE

Birds carry little excess fat so when cachexic their high metabolic rate means they will rapidly catabolize muscle. A small bird of prey can lose pectoral mass within just 2–3 days. Signs of emaciation are a prominent keel bone and translucent skin.

The breeding season is a very energy-expensive time for birds so species build up fat deposits beforehand. Courtship, territorial aggression, mating, nest building, egg formation, and egg laying all draw vast reserves of energy. In addition, incubation and feeding hungry chicks leaves little time for the parent to forage so it can suffer from a shortage of energy. Molting also increases the metabolic rate because birds need to draw on protein and energy for feather regrowth (Blem 2000).

Thermoregulation

Birds regulate their body temperature between 39–42° C, with smaller birds like the passerines having higher body temperatures and large flightless birds like the ostrich falling within the mammalian range (Dawson & Whittow 2000). They have very poor tolerance for high temperatures and 46° C is fatal. Unlike mammals, they have no brown fat but regulate their body temperature by a variety of behavioral and physiological means.

Plumage

Birds use their plumage for both heat loss and heat conservation. The contour feathers provide some insulation but it is the fluffy down feathers underneath that provide most thermal insulation. When cold, birds fluff these feathers to trap air pockets between the feathers and will shiver the pectoral muscles to produce heat. They can also reduce heat loss by 12% by tucking their head under their wing and by 40–50% by sitting down (Dawson & Whittow 2000; Maina 1996; Welty 1982b).

To dissipate heat birds can extend their wings from their body and elevate the scapula feathers to expose the bare skin (*apteria*) of the back of the neck.

Body mass

Birds are extremely sensitive to draughts or poor ventilation as heat loss due to convection means they must increase their metabolic rate. This is particularly severe in small birds as the high ratio of surface area to body mass means body cooling is more rapid. Likewise feather-plucking birds or young chicks are also very vulnerable and need extra nutritional support to avoid negative energy balance.

Fat is a very poor thermal conductor so aquatic birds like penguins which inhabit cold climates have a large subcutaneous layer of fat to insulate against the cold.

CLINICAL NOTE

It is important to avoid too much feather plucking in the surgical patient to prevent heat loss. Use warmed prepping solutions only and avoid surgical spirit as this will also increase evaporative heat loss.

Evaporation

Birds which are overheated can use thermal panting or gular fluttering. Thermal panting increases evaporative loss from the upper respiratory tract and is a highly effective means of heat loss. In fact, the ostrich can maintain a body temperature of 39.3° C by thermal panting, even when the ambient temperature is 51° C (Welty 1982b). Gular fluttering is when the bird vibrates the hyoid muscle and bones in the throat causing evaporation from the lining of the mouth and throat (Dawson & Whittow 2000).

When the bird is expending high energy, that is, when it is flying or running, heat can also be dissipated through the large surface area of the airsacs (Jukes 1971). Flying also exposes the thinly feathered ventral wing and dissipates heat by convection.

Blood shunting

Birds do not have sweat glands but lose heat through their skin or via blood shunts. Some birds, like pigeons and doves, dilate a large vascular plexus on the back of their neck called the *plexus venosus intracutaneous collaris* (Harlin 1994; Hooimeijer & Dorrestein 1997).

A large proportion of the blood from the left ventricle flows to the legs during stress to increase heat loss. In some long-legged species the legs get three times as much blood per heartbeat as the pectoral muscles and twice as much as the brain. Some aquatic and wading birds have countercurrent arteriovenous retes in the proximal feathered part of the leg. These tibiotarsal retes transfer heat from body core arteries to the colder venous vessels bringing blood from the extremities. This enables blood to flow to the legs without detrimental heat loss (West et al. 1981).

Behavior

When they are cold some birds select microclimates to reduce heat loss, like roosting in holes or sheltering in trees. Small birds often huddle together to keep warm. They also adapt their behavior in the heat of the day by seeking shade, bathing or soaring on thermals for cooler air (Dawson & Whittow 2000).

KEY POINTS

- The constraints of flight means there is more morphological uniformity among birds than in reptiles or mammals.
- Fast metabolism, especially in passerines, means birds must eat frequently to maintain energy levels.
- Birds are endothermic, with a body temperature range of 40–42° C.
- Birds conserve heat via insulating plumage and tibiotarsal retes.
- Birds lose heat by exposing bare areas of skin, through the airsacs, panting and gular fluttering, and dilation of superficial blood vessels.

SKELETAL SYSTEM

There are two main subclasses of bird in existence today and these are based on the anatomical structure of the sternum. These are the ratites, which include the flightless emu, ostrich (Fig. 6.3), and kiwi, and the carinates, which include the rest of avian species (8616 species). The largest living carinate is the Andean condor (*Vultur gryphus*) which has a wingspan of 3 m and weighs 15 kg.

Ossification of bones

Like mammals, birds ossify their skeleton on a cartilaginous model although secondary centers of ossification are lacking. The cortex is relatively thin but the medulla is bridged by numerous trabecular struts to add extra strength (Evans 1996; Taylor et al. 1971; Tully 2002).

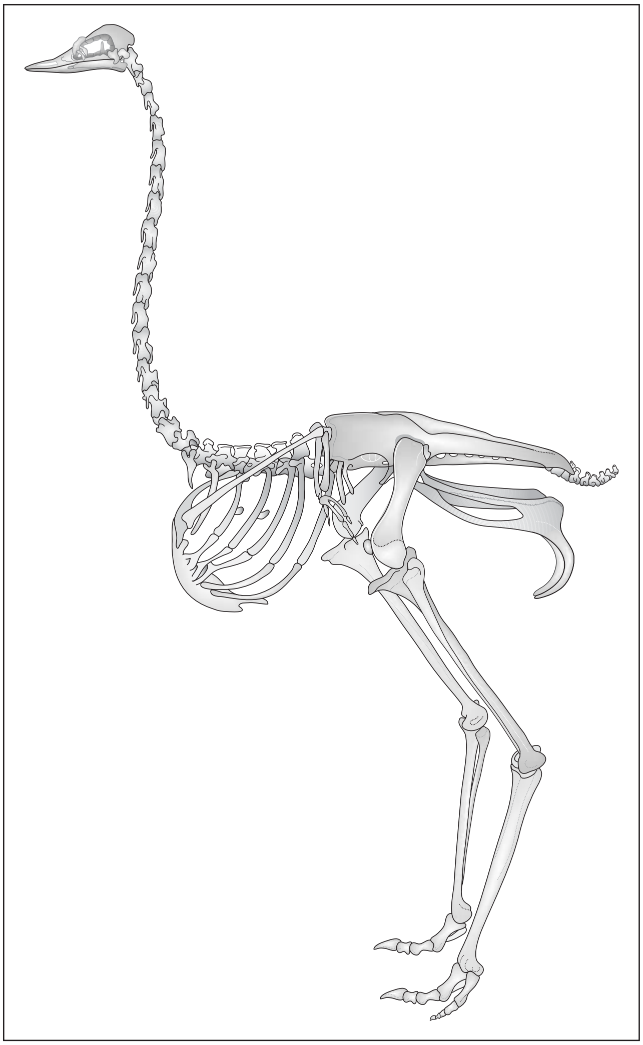


Figure 6.3 • The skeleton of a ratite (ostrich, *Struthio camelus*), showing flat sternum, rudimentary pectoral girdle and vestigial wings. Unlike other avian species the ostrich also has a pubic symphysis which may be an adaptation to support the heavy mass of the viscera.

Cortical bone is similar in both sexes but in the female the medullary cavity is very labile and is the most important calcium reserve for the egg (Taylor et al. 1971; Tully 2002). Prior to laying, medullary bone draws calcium from the alimentary tract to calcify the medullary cavity (Johnson, AL 2000). Bony trabeculae are laid down from the endosteum and the total skeleton increases by about 20%. This phenomenon, called *polyostotic hyperostosis*, is visible radiographically and is followed by bone resorption once the eggshell is calcified (Fig. 6.62).

CLINICAL NOTE

The thin avian cortices and internal bone struts mean that bones can splinter very easily, making orthopedic surgery a challenge at times (Orosz 2002).

Skeletal modifications for flight

- Birds have a lightweight fused skeleton. For example, the skeleton of a pigeon is 4.4% of body mass compared to that of a rat's skeleton which is 5.6% (King & King 1979; Maina 1996) (Fig. 6.4).
- The avian forelimb is modified into a wing while the bill and neck are modified for food prehension. The manus is tapered and fused to hold the primary feathers (Figs. 6.5 and 6.6).
- Many bones of the backbone and limbs are fused to form a rigid and strong but light framework. The fused rib cage helps resist the twisting and bending of wings in flight while the rigid pectoral girdle acts like a wing strut. A fused tail vertebra (pygostyle) provides a short tail for steering and maneuverability. The sternum is keeled (carinate) to hold the muscles of flight (King & Custance 1982; King & King 1979).
- The airsacs extend into the medullary cavity of the major bones, such as the humerus, coracoid, pelvis, sternum, and vertebrae. They are most developed in the good fliers to help in weight reduction. In some birds the femur, scapula and furcula are also pneumatized but this does not tend to happen to the distal bones. The skull also consists of a honeycomb of air spaces with delicate spicules for support (Koch 1973; Maina 1996).
- The supracoracoid muscle lifts the wing by passing from its ventral attachment on the sternum through the triosseal foramen to insert on the dorsal humerus. This keeps all the heavy flight muscles along with the muscular gizzard situated ventrally at the bird's center of gravity (King & Custance 1982).

Skull

The cranial bones of the skull are fused to form a rigid, but lightweight, box with large orbits separated by a thin, bony

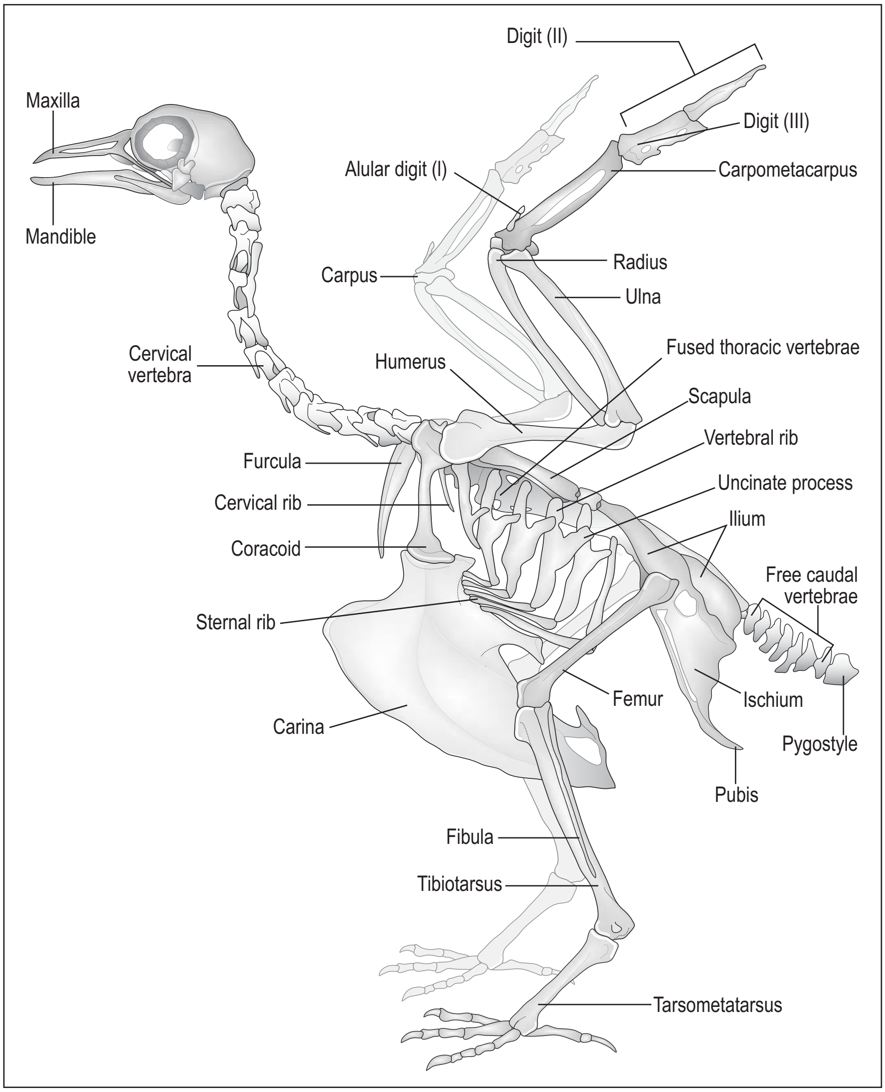

Digit (II)
Maxilla
Digit (III)
Alular digit (I)
Carpometacarpus
Mandible
Radius
Carpus
Ulna
Fused thoracic vertebrae
Cervical vertebra
Humerus
Scapula
Vertebral rib
Furcula
Uncinate process
Cervical rib
Ilium
Coracoid
Free caudal vertebrae
Sternal rib
Femur
Ischium
Carina
Pygostyle
Pubis
Fibula
Tibiotarsus
Tarsometatarsus

Figure 6.4 • The skeleton of a carinate, the pigeon, showing modifications for flight: large keeled sternum for flight muscles, fused thoracic vertebrae, strong pectoral girdle for bracing the wings and large feet to withstand the concussion of landing.

interorbital septum (Figs. 6.10–6.12). The brain has been pushed caudally and ventrally into the occipital region and lies at a 45-degree angle tilt. A single occipital condyle articulates with the atlas, allowing birds to rotate their neck to an angle of 180 degrees (Dyce et al. 2002; Koch 1973).

Within the rostral skull there are large areas of honeycomb pockets of air or sinuses that are especially prominent in flighted birds. The infraorbital sinus has many diverticula and is very well developed in psittacines. Diving birds and birds that peck at hard objects (e.g., woodpeckers) lack these pneumatic zones in order to help the skull withstand more concussive force.

Cranial kinesis

Birds, especially psittacines, have a highly mobile kinetic skull. This means that, unlike mammals that can only move their bottom jaw, they are also able to move their maxillary jaw (upper beak). This wide gape is achieved by an elastic hinge at the rostral skull that allows the bones to bend without disturbing the cranium (Fig. 6.7). In psittacines, this elastic hinge is replaced by an articular craniofacial joint, allowing parrots even more flexibility of movement (Evans 1996; Quesenberry et al. 1997).

The mobile quadrate bone also plays a major role in skull kinesis. This bone not only articulates with the cranium but also with the premaxilla via two rodlike thin bones called the jugal arch (precursor of the zygomatic bone) and pterygoid–palatine bone. When the jawbone is lowered the quadrate bone pushes these two bones rostrally to elevate the upper jaw, allowing the bird a wide gape (Evans 1996; Maina 1996).

Premaxilla

The upper jaw is derived from the premaxillary and nasal bone and a small part of the maxillary bone. This is very thin and lightweight, owing to the diverticula extending from the infraorbital sinus. The kinetic movement of this upper jaw is either prokinetic or rhynchokinetic. In prokinetic birds, like psittacines and chickens, the upper jaw moves as a unit and the nasal openings are small and oval (Fig. 6.8). In rhynchokinetic birds (e.g., pigeons and waterfowl) only the rostral part of the upper jaw moves and the nasal openings are elon-

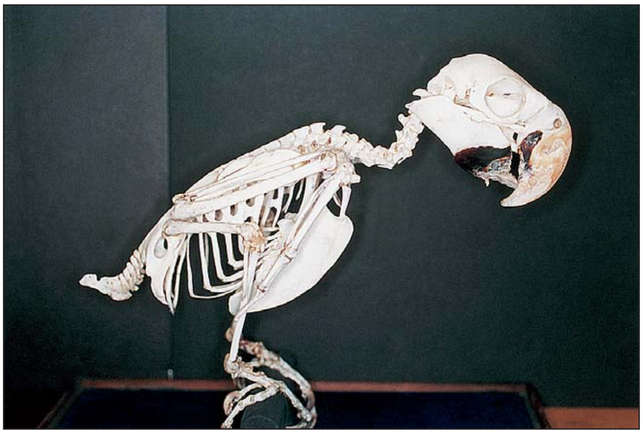


Figure 6.5 • Skeleton of Blue and gold macaw (*Ara ararauna*). Note the s-shaped neck, the powerful beak (the lower beak is damaged in this specimen) and complete orbit of the psittacine.

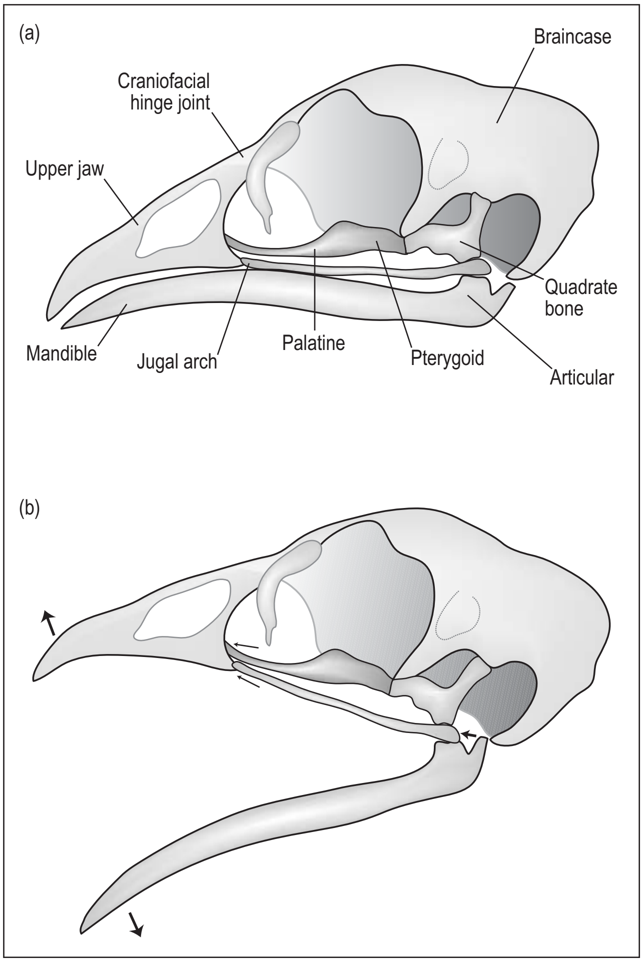

(a)
Braincase
Craniofacial hinge joint
Upper jaw
Quadrate bone
Mandible
Jugal arch
Palatine
Pterygoid
Articular
(b)

Figure 6.7 • Cranial kinesis.
(a) Skull of domestic fowl (*Gallus gallus*) with mouth closed.
(b) Open mouth view. When the jawbone is lowered the quadrate bone pushes the jugal arch and pterygoid-palatine bone rostrally to elevate the upper jaw, allowing the bird a wide gape.

Figure 6.6 • Blue and gold macaw (*Ara ararauna*).

gated and slitlike (King & McLelland 1984; Quesenberry et al. 1997) (Fig. 6.9).

Mandible

The mandible in birds consists of five small bones which fuse caudally with the articular bone. The most rostral bone is the dentary bone and this forms a fully ossified mandibular symphysis. The others are the surangular, angular, splenial and prearticular. Caudally, the articular bone articulates with the quadrate bone. In mammals these two bones have evolved into the auditory bones incus and malleus.

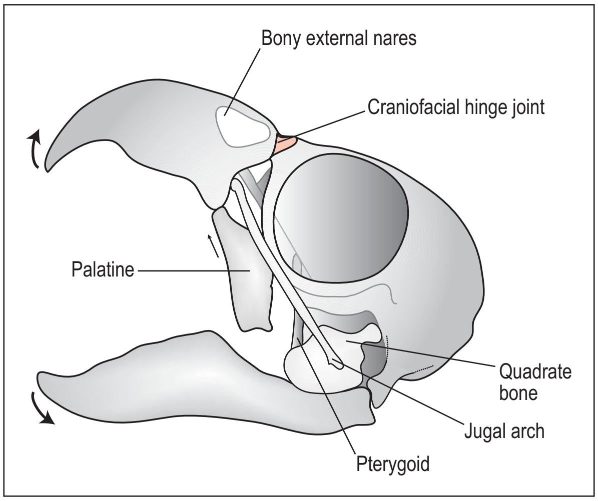

Bony external nares
Craniofacial hinge joint
Palatine
Quadrate bone
Jugal arch
Pterygoid

Figure 6.8 • Prokinesis.
The upper jaw moves as a unit and the nasal openings are small and oval. This is particularly developed in psittacines, which have a craniofacial hinge.

KEY POINTS

- Avian skull is highly kinetic
- Movable quadrate bone allows wide gape
- Single occipital condyle so can rotate head 180 degrees
- Well-developed sinuses
- Psittacines have synovial joint at craniofacial maxillary hinge for greater gape

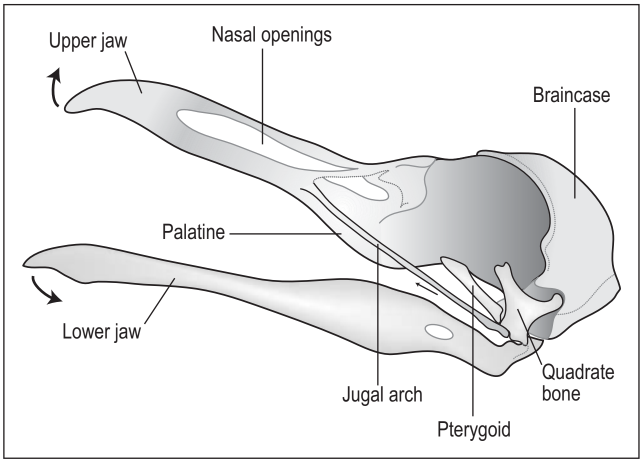

Upper jaw
Nasal openings
Braincase
Palatine
Lower jaw
Jugal arch
Pterygoid
Quadrate bone

Figure 6.9 • Rhynchokinesis.
In birds like pigeons and waterfowl only the rostral part of the upper jaw moves and the nasal openings are elongated and slitlike.

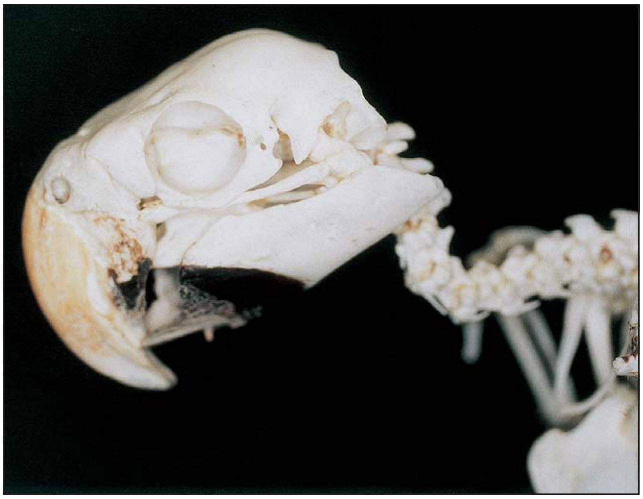


Figure 6.10 • Psittacine skull showing complete orbits and powerful beak.

Axial skeleton

Birds have epaxial muscles dorsally and hypaxial muscles ventrally along the vertebral column. These are most developed in the neck for preening and the apprehension of food. The tail muscles are also well developed for fine control of the tail feathers. The number of vertebrae can vary widely according to species, as can be seen in Table 6.2.

Cervical vertebrae

The forelimbs are modified for flight so the neck and beak play a larger role in grooming and manipulation of objects. In general, necks tend to be longer in waterfowl, which need to be able to reach the uropygial gland for preening.

The cervical vertebrae are long and flexible (numbering from 8 in small birds to 25 in swans) with highly mobile, saddle shaped, articular surfaces enabling it to adopt the

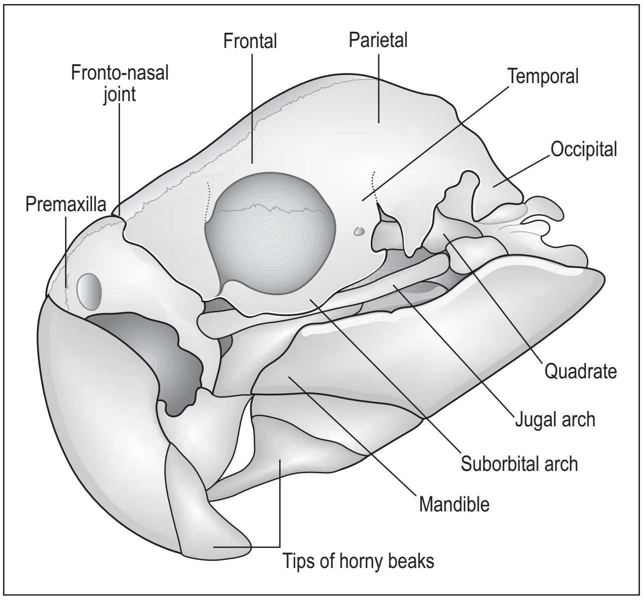

Frontal
Parietal
Fronto-nasal joint
Temporal
Occipital
Premaxilla
Quadrate
Jugal arch
Suborbital arch
Mandible
Tips of horny beaks

Figure 6.11 • Psittacine skull.

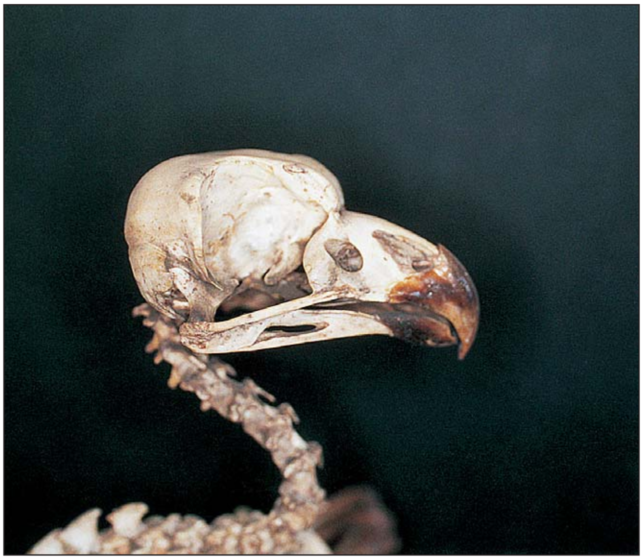


Figure 6.12 • Skull of eagle owl (*Bubo bubo*) demonstrating large incomplete orbits and powerful hooked beak for tearing at prey.

Table 6.2 Number of vertebrae in common avian species (Evans 1996; Koch 1973)

	Cervical	Thoracic	Synsacrum	Coccygeal
Pigeon	12	7 (Notarium)	Fused	8
Chicken	14–17	7 (Notarium)	Fused (15–16)	5–6
Geese	17–18	9	Fused	8
Duck	14–15	9	Fused	8
Budgie	12	8	Fused	8

sigmoid shape bend. Rostrally, the atlas articulates in a ball and socket joint with a single occipital condyle giving head movement great flexibility (Maina 1996). This allows the bird to rotate its head to compensate for poorly developed eye muscles. The caudal cervical vertebrae have rudimentary ribs which are the site of attachment of the cervical muscles (King & McLelland 1984; Koch 1973).

CLINICAL NOTE

The soft tissues of the neck, the esophagus, and trachea are shorter than the cervical vertebrae, so it is impossible to stretch a bird's neck out completely. This sigmoid neck acts like a spring to protect the head and brain from concussive forces while landing. Hence the elegant s-shaped neck of the swan (Koch 1973) (Fig. 6.13).

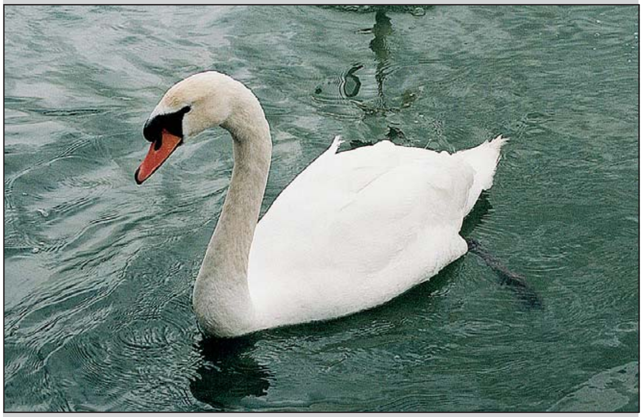


Figure 6.13 • Mute swan (*Cygnus olor*) showing 's'-shaped neck.

Thoracic vertebrae

In birds, much of the lower vertebrae can be fused to confer rigidity on the skeleton for flight. Many species, like chickens, hawks, and pigeons, have the first 3 to 5 thoracic vertebrae fused into a single bone, the notarium, which provides a rigid beam to support flight (King & McLelland 1984; Koch 1973). This is followed by the only mobile vertebra of the trunk. This can be a weak link because, when ventrally displaced, it causes spondylolisthesis or "kinky back" in broilers (Dyce et al. 2002). Budgies have mobile thoracic vertebrae at T6-7 (Evans 1996).

Thoracic vertebrae vary in number from 3 to 10 and can be identified by ribs, which articulate with the sternum. Some cranial and caudal ribs lack a sternal attachment but have a ligamentous attachment instead. External and internal intercostal muscles lie between each rib. A unique feature of avian ribs is a backward-pointing process, the uncinate process, which extends caudodorsally from every rib. This provides attachment for muscles which extend ventrocaudally to the rib behind, adding strength to the thoracic wall and acting like a protective brace around the chest and heart. These are particularly well developed in diving birds such as guillemots to help the thorax withstand the pressure of a dive.

CLINICAL NOTE

In psittacines the last rib does not possess an uncinate process so this provides a useful surgical and laparoscopic landmark (Quesenberry et al. 1997).

Synsacrum

This contains from 10 to 23 vertebrae and is the fusion of caudal thoracic, lumbar, sacral, and caudal vertebrae. It supports the pelvic girdle and hence the bird's entire mass (Fig. 6.15).

Caudal vertebrae

The tail is short and the last vertebrae are fused into a single, flattened bone called the pygostyle, which supports the tail feathers (Fig. 6.14). This is most highly developed in birds that use their tail for climbing and support. Well-developed muscles are present to help control the pitch during flight (King & King 1979; King & McLelland 1984).

Sternum

This is much more extensive than in mammals, being a ventral plate of bone providing protection. The keel bone (*carina*) provides the main attachment for the flight muscles. It is most developed in sophisticated fliers like swifts and hummingbirds and least developed in the flightless ratites, which have a flat and raft-like sternum (Bezuidenhout 1999; King & McLelland 1984; Maina 1996).

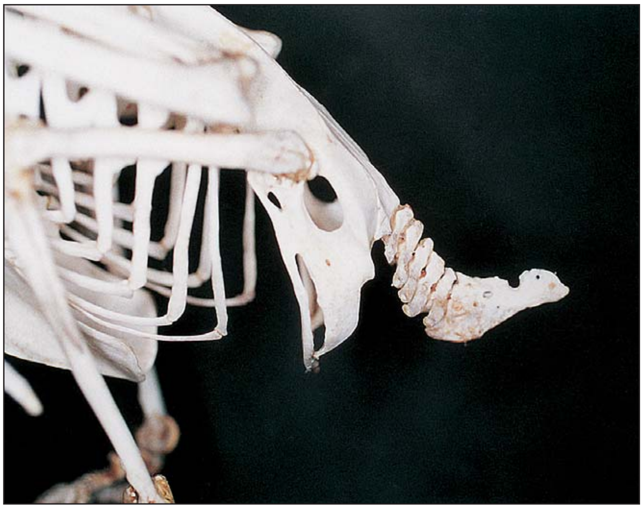


Figure 6.14 • Lateral view of psittacine pelvis, caudal vertebrae and pygostyle.

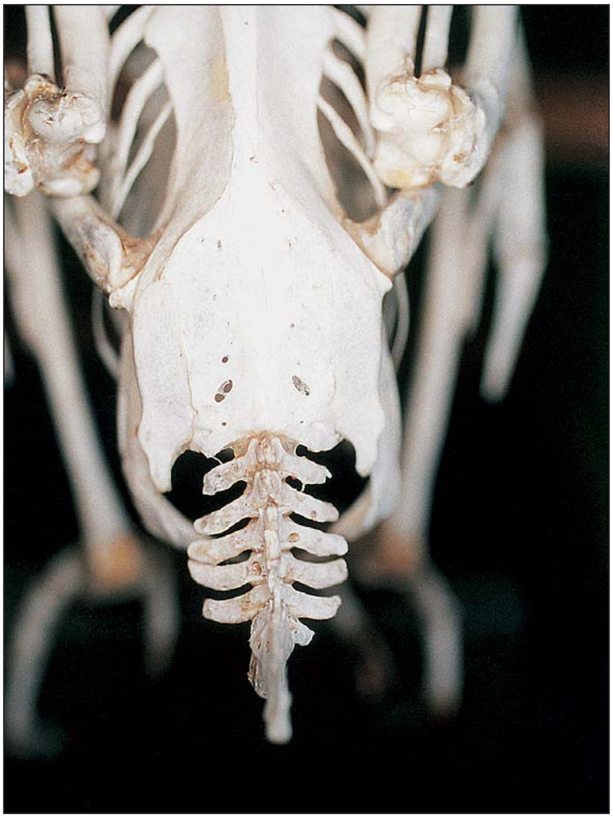


Figure 6.15 • Dorsal view of psittacine synsacrum, pelvis, caudal vertebrae and pygostyle.

The caudal portion of the sternum is often notched or perforated by windows. These are areas of the sternum that have failed to ossify and are lined by fibrous membranes. They are most developed in poor fliers like poultry (Dyce et al. 2002; Koch 1973).

Appendicular skeleton

Pectoral girdle

This consists of the clavicle, coracoid, and scapula, all of which articulate proximally to form the triosseal foramen. Distally, the scapula and coracoid also form the glenoid cavity, which is shallow and directed laterally to allow the wings adduct and abduct for flight (Evans 1996) (Fig. 6.16).

Clavicle

Along with the coracoid, this acts to brace the wing and is the proximal attachment of the pectoralis muscle. These are rudimentary in many Psittaciformes and Strigiformes (Evans 1996; King & McLelland 1984). In many species the two clavicles are fused into the furcula (wishbone) for extra strength. This unites both shoulder blades and has a springlike function (Koch 1973).

Coracoid

This is a short, strong bone which extends from the sternum and acts like a wing strut in preventing the wing muscles from compressing the thorax on the downstroke (King & McLelland 1984). It lies deep below the cranial edge of the pectoralis muscle and lateral to the jugular veins and subclavian and common carotid arteries.

Scapula

This is a long blade-like bone whose length varies with the flying strength of each species. It lies parallel to the backbone and extends as far caudally as the pelvis.

Pelvic girdle

The pelvic girdle rotates backward and functions for perching and locomotion like running and swimming. It is made up of a fusion of the ischium, pubis, and ilium and is rigidly

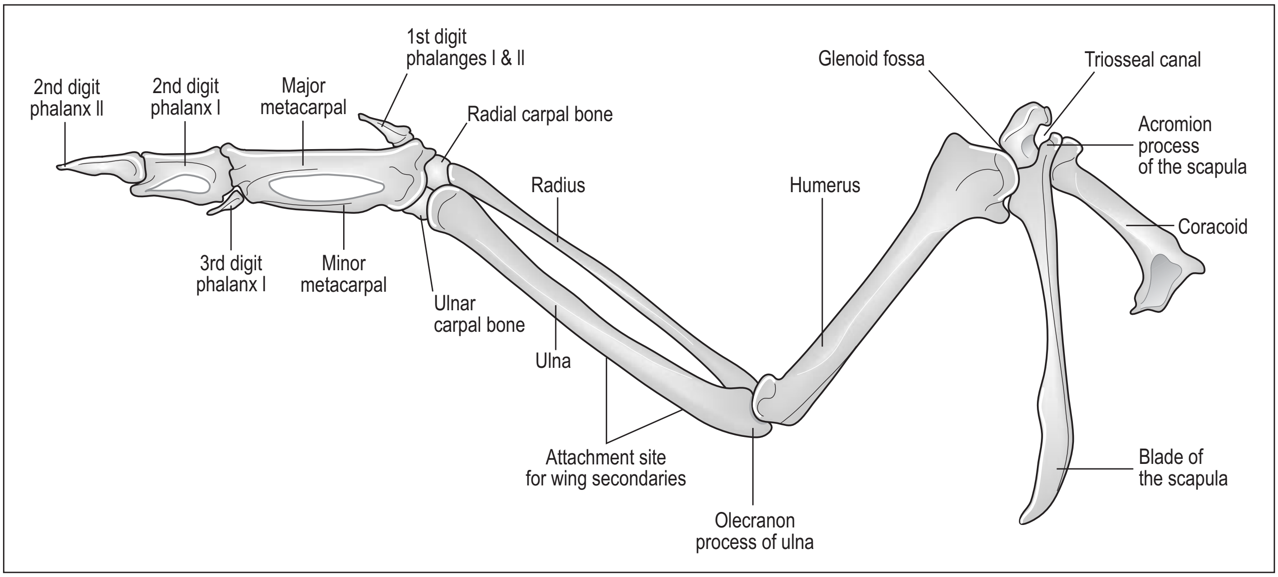

1st digit phalanges I & II
2nd digit phalanx II
2nd digit phalanx I
Major metacarpal
Radial carpal bone
Glenoid fossa
Triosseal canal
Acromion process of the scapula
Radius
Humerus
Coracoid
3rd digit phalanx I
Minor metacarpal
Ulnar carpal bone
Ulna
Attachment site for wing secondaries
Blade of the scapula
Olecranon process of ulna

Figure 6.16 • Ventral view of pectoral girdle and left wing.

CLINICAL NOTE

As the coracoid bone acts as the brace between wing and sternum it is commonly damaged during wing trauma. If the wing is drooping and the humerus feels intact, radiography may be necessary to check the coracoid bone for fractures.

fused to the synsacrum at the ilium. In most species it is incomplete ventrally, presumably to allow for passage of eggs through the pelvic canal (King & Custance 1982). The exceptions are the ostrich and rhea, which have a pubic symphysis that may be an adaptation to support the heavy mass of viscera (Bezuidenhout 1999; Evans 1996; Koch 1973; Maina 1996; Raikow 1985) (Fig. 6.17).

The acetabulum is deep and, as there is a strong femoral attachment, luxation is uncommon (Quesenberry et al. 1997). The trochanter of the femur also articulates with the antitrochanter of the ilium and this additional joint enables birds to perch on one leg very easily (Maina 1996). Ventrally there are bilateral renal fossae for the caudal division of the kidneys.

Wings

The wing skeleton consists of humerus, radius, ulna, carpal bones, carpometacarpus, and three digits (Orosz et al. 1992).

Humerus

The humerus is a short bone that lies against the body wall when the wing is folded. Proximally, it has a well-developed pectoral crest where the pectoralis muscles insert. The biceps brachii lies along the cranial humerus and serves to flex the wing while the triceps brachii lies caudally and serves to extend the wing. The clavicular airsac extends into the medullary cavity, making this bone pneumatic.

Radius and ulna

These are long bones that lie parallel to each other. In birds, these bones do not twist and the ulna, which lies caudally, is the bigger bone. Small bony knobs can be seen on the caudal aspect where the secondary flight feathers insert.

Manus

The wrist and hand are severely reduced to provide a strong base for the attachment of the primary flight feathers. Only

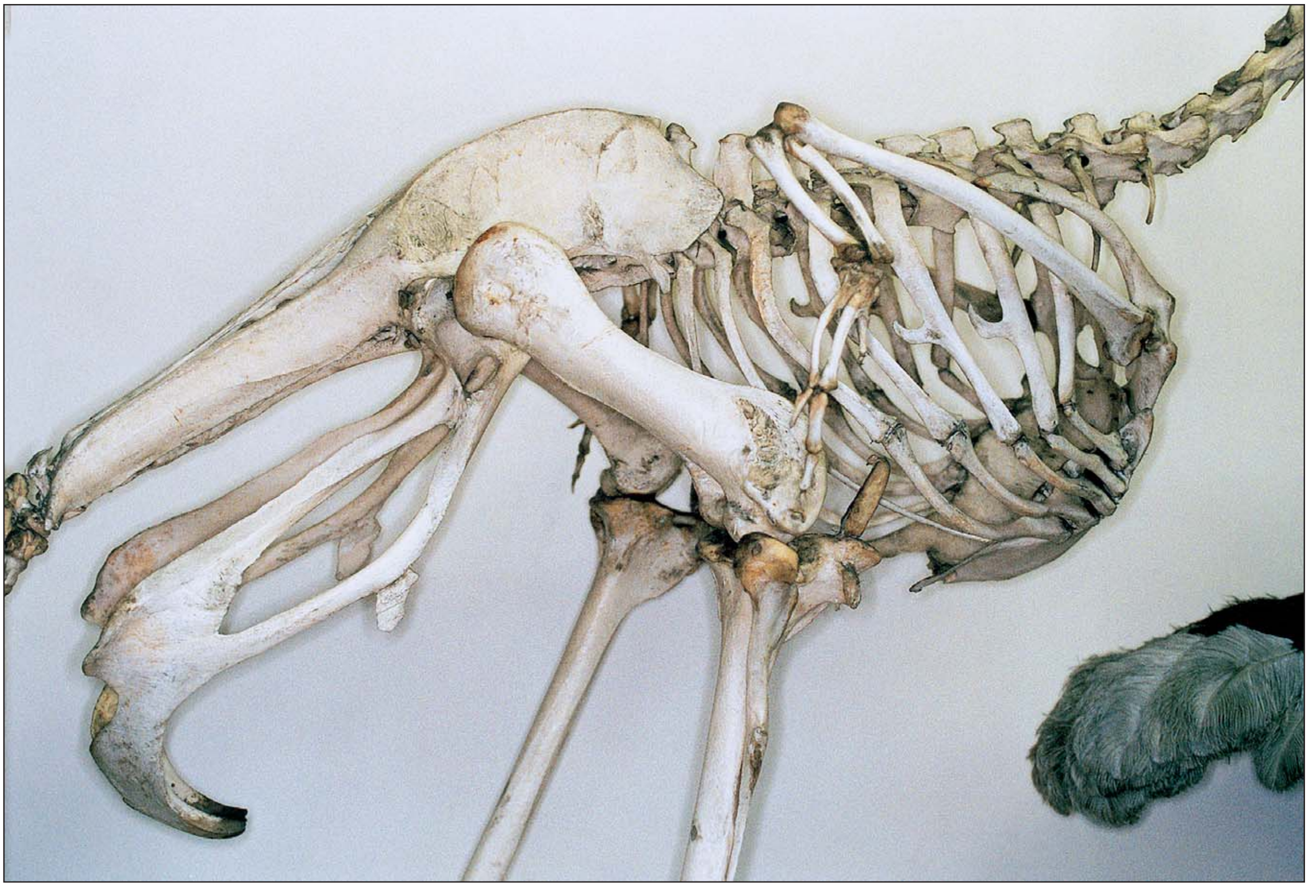


Figure 6.17 • Sternum and pelvis of ostrich (*Struthio camelus*). The pubic symphysis may be an adaptation to support the heavy mass of viscera in these species.

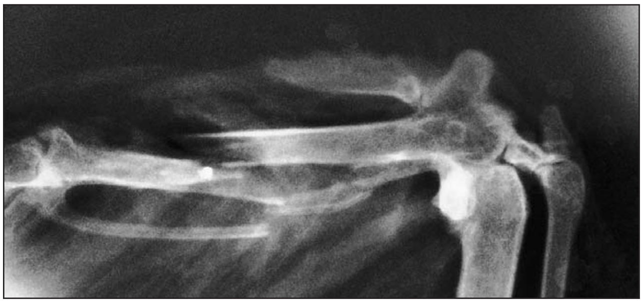


Figure 6.18 • Radiograph of distal wing of Buzzard (*Buteo buteo*) with major and minor metacarpals fractured by lead shot.

CLINICAL NOTE

The secondary flight feathers insert onto the caudal ulna bones. The distal ulna is also the site for placement of intraosseous catheters.

the ulnar and radial carpal bones remain to form the proximal carpus, which is then attached to the carpometacarpus. There are three digits. The first digit is the alular digit and can have 1 or 2 phalanges. This forms the "bastard wing" and is more mobile than the rest. Feathers attached to this digit are raised during flight to prevent stalling at slow speeds (Orosz 2002).

The major metacarpal bone articulates with the major or second digit, which has two phalanges, while the minor metacarpal bone articulates with the minor or third digit (Fig. 6.18). The carpus and elbow joints are restricted only to extensions and flexion in order to provide a rigid wing surface. They flex simultaneously to fold the wing (Orosz 2002; Orosz et al. 1992).

Pinioning

This is when the manus is cut off at the carpus on one wing to prevent flight. It is frequently done in waterfowl collections at between 4 to 10 days of age. The alular digit is preserved and a cut is made through the two metacarpals as close as possible to the carpus (Dyce et al. 2002; King & McLelland 1984).

Wing types

Four basic wing types can be identified: elliptical, broad, narrow and tapered (Fig. 6.20, Table 6.3). Passerines and pigeons maneuver through undergrowth and have short, broad elliptical wings with rapid beats. They have a large alula and wing slots to prevent stalling at low speeds. Eagles and vultures have a long broad wing that enables them to soar at low speeds. These birds have a large alula and wing slots. Ocean-going birds like gulls and gannets have a long, narrow, and pointed wing with no wing slots, allowing them to soar at high speeds. Swifts and falcons have a tapered wing with no wing slots, which allows them to fly with rapid wing beats at high speeds (King & King 1979; King & McLelland 1984; Maina 1996).

HOW DO BIRDS FLY?

Contrary to popular belief, birds fly in a very different manner to airplanes as their wings provide not just the lift but the propulsive force as well. It is the primary wing feathers which provide most of this propulsion and the secondaries that provide the lift, which is why pinioning of waterfowl is so successful. Smaller birds become rapidly airborne, but large birds like the swan have to "taxi" along the water before they can take off (Spearman & Hardy 1985).

The dorsal surface of the bird's wing is convex and the ventral surface is concave. The leading edge is thickest where bones and muscles provide strength and tapers caudally to the trailing edge. Air traveling over the dorsal wing has to travel further than air passing ventrally and this increased speed produces low pressure dorsally. As the air passes over it generates an upward force called lift. This aerodynamic force is what enables the bird to rise into the air and defy gravity (Spearman & Hardy 1985).

If the leading edge of the wing is tilted the lift force is increased. Wing control is achieved by changes in position of the wings and slots between the feathers (Fig. 6.19). To avoid stalling at low speeds, slots are formed by the separation of the primary feathers and the alular or bastard wing. These slots let through some air to maintain a smooth stream on the upper surface so as to increase lift.

A drag force opposes the forward motion and reduces the lift. The aerofoil design of the bird's wing provides maximum lift and minimum drag.

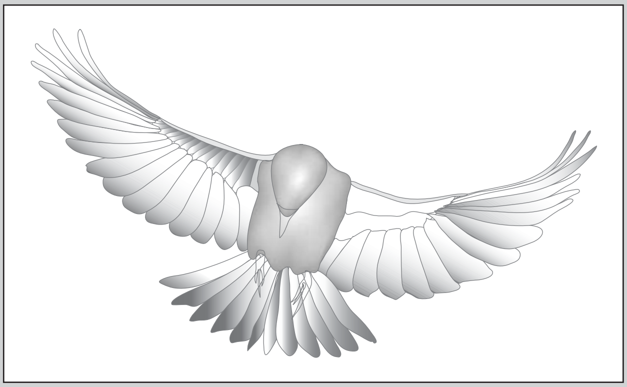


Figure 6.19 • Flighted bird about to land.

Musculature

The main bulk of muscles in flying birds is concentrated in the pectoral muscles, which can represent up to one third of body mass. This concentration of the muscle mass ventrally, near the center of gravity, provides stability for flight.

Unlike mammals, birds have a very sparse dorsal musculature as the axial skeleton is so tightly fused together that little muscle support is necessary. The muscles of the limbs and wings are also sparse, with many lightweight tendons

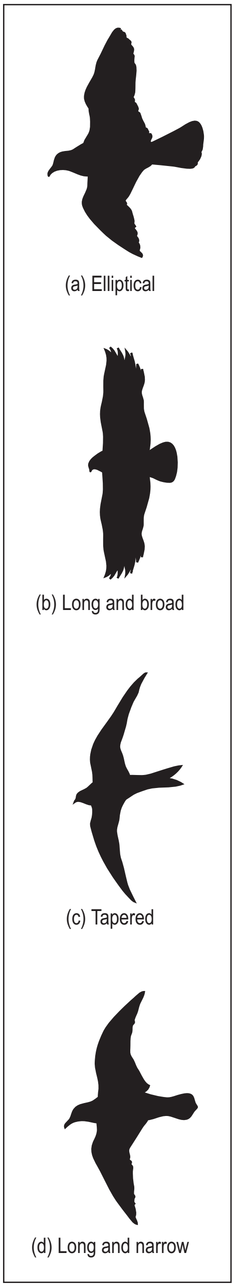

(a) Elliptical
(b) Long and broad
(c) Tapered
(d) Long and narrow

Figure 6.20 • Comparison of four basic wing types.
(a) Elliptical
(b) Long and broad
(c) Tapered
(d) Long and narrow

Table 6.3 Wing shape in relation to type of flight (King & McLelland 1984)

Wing type	**Type of species**	**Type of flight**
Elliptical, short & broad (wing slots)	Passerines, pheasants, pigeons	Rapid wing beat
Long and broad (wing slots)	Vultures, eagles, pelicans	Low speed soaring
Tapered (no wing slots)	Swifts, falcons, hummingbirds, terns	Rapid, high-speed wing beat
Long, narrow and pointed (no wing slots)	Albatrosses, gulls, gannets	High-speed soaring

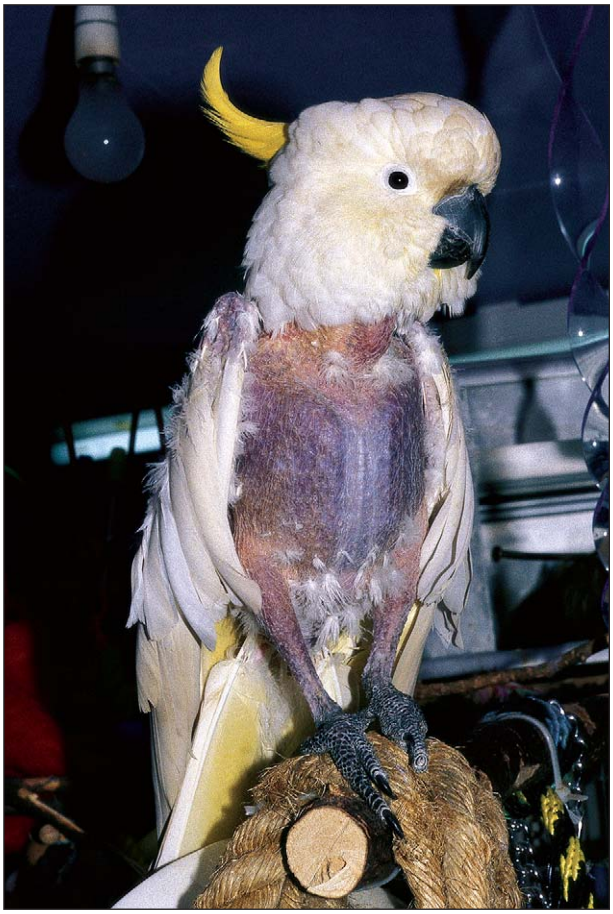


Figure 6.21 • Flighted birds like this Sulphur-crested cockatoo (*Cacatua sulphurea*) have a high level of myoglobin in the pectoral muscles. The breast muscles appear red in contrast to the white breast muscles of the flightless chicken. (Photo by Claire Nuttall.)

(Koch 1973). Birds like swifts, which rarely land, have practically redundant leg musculature, while the flightless ostrich has large leg muscles to help them run at high speeds.

Avian muscles have a mixture of both white and red muscles. Red muscle appears red due to the abundance of the oxygen-carrying pigment myoglobin and has an extensive blood supply. As these utilize aerobic metabolism, which can work for long periods, it is found in flight muscles. White muscle is powered by anaerobic metabolism, which is good for rapid contractions, but it tires easily due to lactic acid build up (King & McLelland 1984).

The function of the muscle can be identified by its color (Fig. 6.21). For example, we all know the flightless chicken has white breast muscle and a darker colored drumstick. This is because the gastrocnemius leg muscles contain ten times more myoglobin than the breast. The flighted pigeon, conversely, has pectoralis muscle containing 40 times more myoglobin than chicken muscle (Dyce et al. 2002).

Muscles of flight

The muscles of flight are the pectoralis and the supracoracoid muscles and can represent about 20% of body mass.

The pectoralis provides the powerful down stroke and the supracoracoid provides the upstroke (Raikow 1985). Flightless birds have a poorly developed keel bone and, hence, pectoral muscles.

The pectoral muscles extend from the sternum to insert on the medial pectoral crest of the humerus. In most birds like Psittaciformes, Falconiformes, and Columbiformes, the superficial pectoral muscles form the main pectoral mass as they create the downstroke and are consequently essential for flapping flight. Birds like vultures and ocean going seabirds, which glide and soar over long distances, have a well-developed deep pectoral muscle to help brace the wing against the force of wind and keep it motionless while gliding (King & King 1979; Orosz 2002; Orosz et al. 1992).

The supracoracoid muscle also attaches to the ventral sternum beneath the pectoral muscles (Fig. 6.22). Its tendon then runs dorsally through the triosseal canal to insert on the dorsal tubercle of the humerus. By this method, a muscle lying below the wing can elevate the wing for flight and this keeps the mass of the bird stable. This muscle is used mainly for takeoff and is not necessary while in flight. It is particularly developed in species that hover and perform steep takeoffs (King & Custance 1982; King & McLelland 1984).

The tail acts as a rudder and brake. The tail feathers are attached to the pygostyle and radiate from it like a fan. Each feather can both move individually or as a whole, giving the bird fine control during flight. They can fan out to create drag and slow the bird down or twist to cause turning in flight (King & McLelland 1984; Raikow 1985).

CLINICAL NOTE

The pectoral muscles can be palpated to assess body condition and are also a site for intramuscular injections. However, pectoral injections should be avoided in birds relying on 100% flight efficiency: for example, birds of prey or wild birds due to be released.

Many birds (such as Galliformes) have fenestrated sternums, so when making intramuscular injections introduce the needle cranially, parallel to the sternum, to avoid puncturing the liver.

Propatagium

This triangular fold of skin extends from the shoulder to the carpus and forms the leading edge of the wing. It consists of thin dorsal and ventral layers of skin with a strong ligament running along the edge. This *ligamentum propatagiale* arises proximally on the deltopectoral crest and inserts onto the extensor process of the carpometacarpus. It has collagen at each end, is elastic in the middle and, when tensed, helps

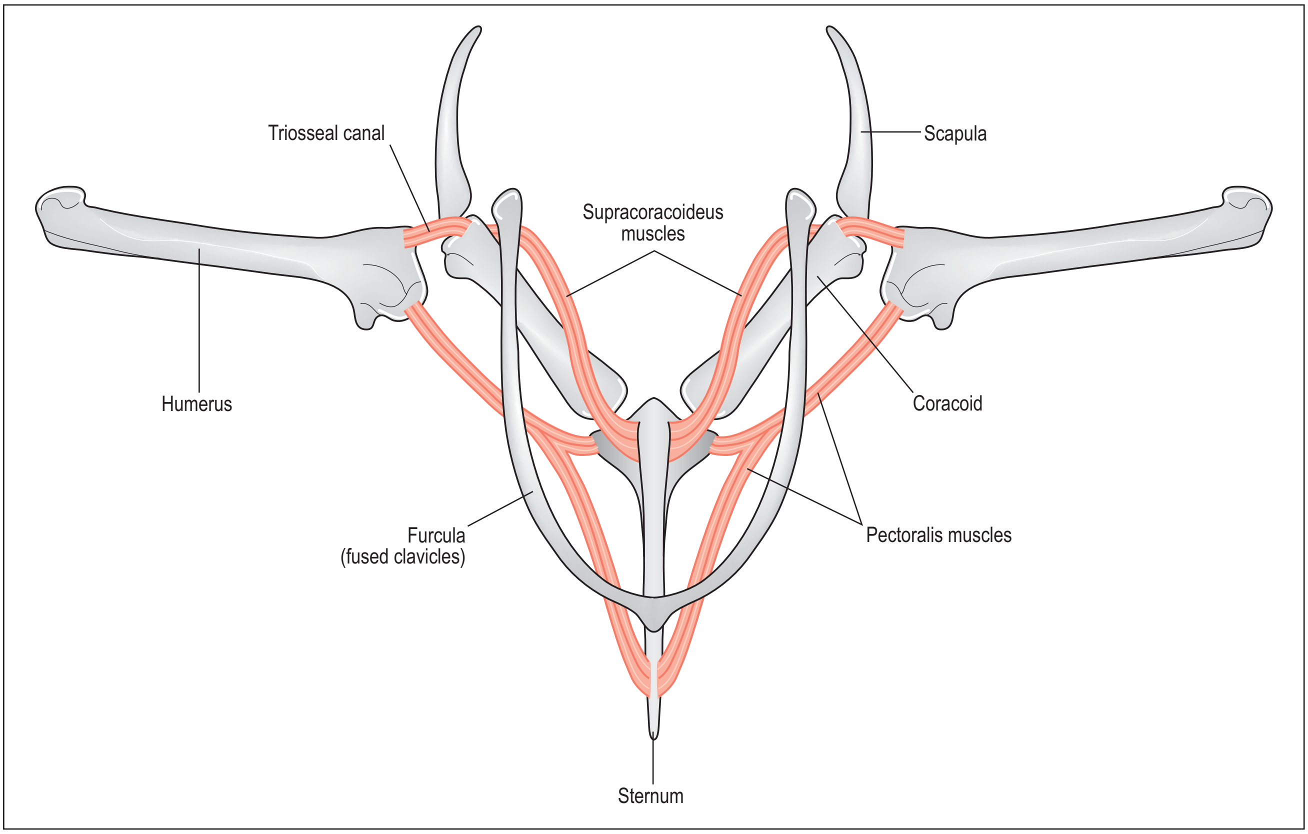


Figure 6.22 • Diagram of pectoral muscles demonstrating how both the supracoracoideus, which elevates the wing, and the pectoralis, which depresses the wing, have ventral origins. This keeps the heavy musculature close to the bird's center of gravity.

to achieve smooth airflow. Elastic branches fan out from the elastic part of the ligamentum and across the propatagium to insert on the dorsal antebrachial fascia of the distal ulna. In some large raptors a support ligament runs parallel to this tendon to give additional support when the wing is extended (Brown & Klemm 1990).

CLINICAL NOTE

The propatagium, along with feathers, is essential for producing aerodynamic lift for flight. Propatagial tears or injury to the propatagial ligament are very difficult to repair and can render the bird flightless (Brown & Klemm 1990; Orosz 2002).

Pelvic limbs

The pelvic limb has been fused distally to absorb the shock of takeoff and landing (Figs. 6.23 and 6.24). It consists of femur, tibiotarsus, fibula, tarsometatarsus, metatarsal bone, and in most birds, four digits. It is covered by feathers and skin as far as the level of the intertarsal joint and is followed by scales below. In general the pelvic limb is not involved in flight and is used more for swimming, catching prey, and wading (Orosz et al. 1992) (Fig. 6.25).

Femur

This is a short bone that slopes cranially (almost horizontally) in order to ensure that the large feet lie under the bird's center of gravity. It articulates with the tibiotarsus and the

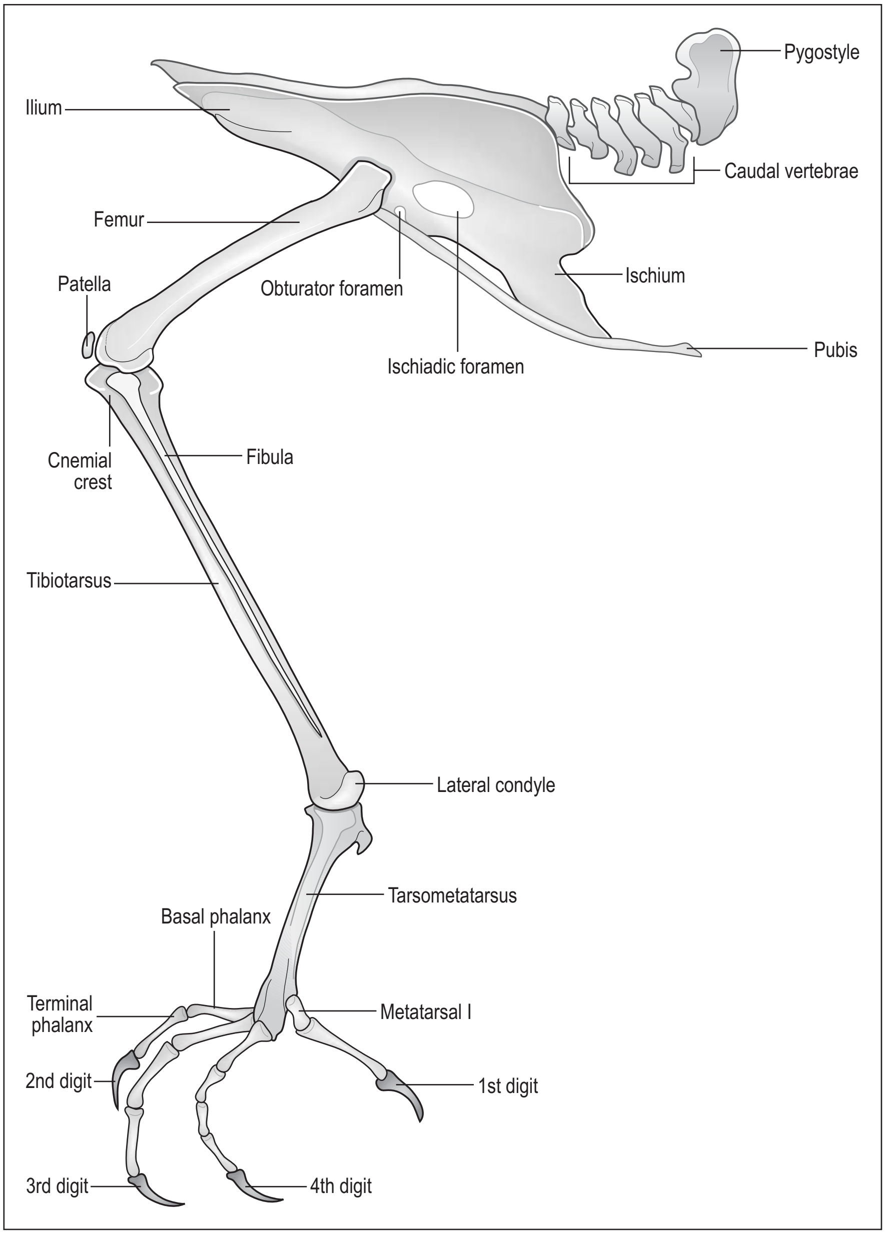

Pygostyle
Ilium
Caudal vertebrae
Femur
Patella
Obturator foramen
Ischium
Pubis
Ischiadic foramen
Cnemial crest
Fibula
Tibiotarsus
Lateral condyle
Tarsometatarsus
Basal phalanx
Terminal phalanx
Metatarsal I
2nd digit
1st digit
3rd digit
4th digit

Figure 6.23 • Lateral view of pelvic limb.

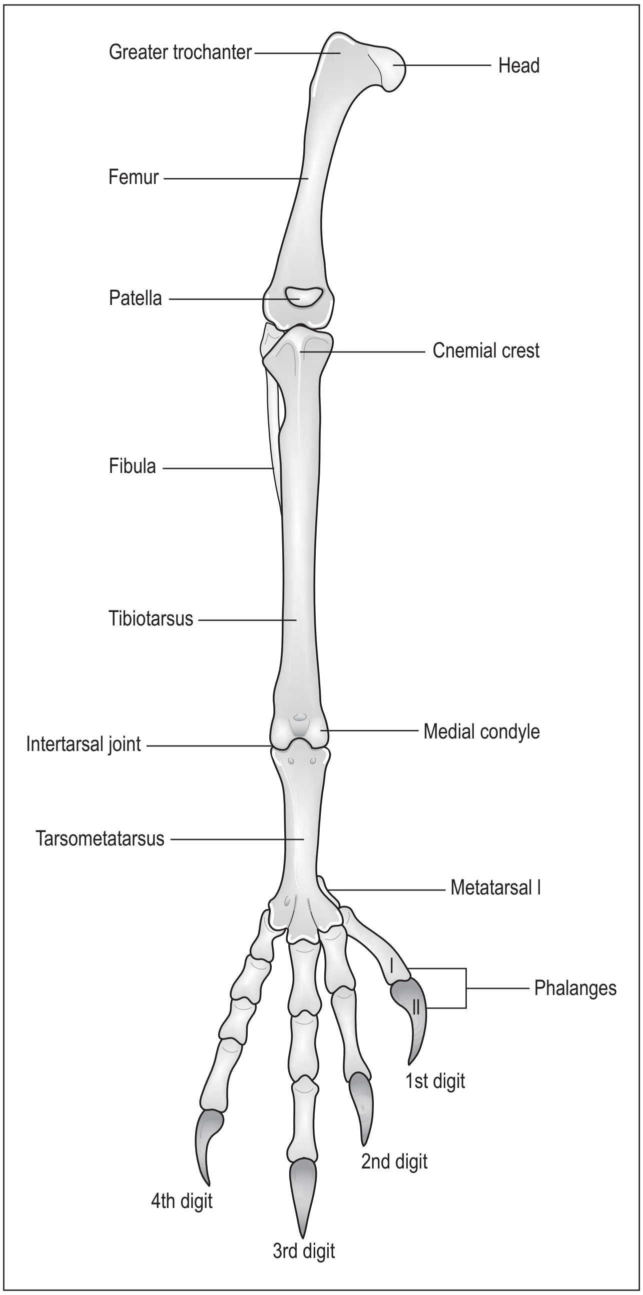

Greater trochanter
Head
Femur
Patella
Cnemial crest
Fibula
Tibiotarsus
Intertarsal joint
Medial condyle
Tarsometatarsus
Metatarsal I
I
II
Phalanges
1st digit
2nd digit
4th digit
3rd digit

Figure 6.24 • Cranial view of right pelvic limb.

patella. As in mammals, the knee joint has two menisci, cranial and caudal ligaments, and collateral ligaments (Harcourt-Brown 1996). The femorotibialis muscle (the equivalent of the mammalian quadriceps) acts to extend the knee joint, and the patella is a sesamoid in its tendon of insertion. The main movements are flexion and extension.

Tibiotarsus

The tibiotarsus is the fusion of the tibia and proximal tarsal bones and is commonly called the drumstick in poultry. It is the largest bone on the pelvic limb (Evans 1996). A cranial crest known as the *cnemial* crest lies at the proximal tibia.

WHY DOES A DUCK WADDLE?

When birds walk they lean outwards to bring the center of gravity above the foot on the ground while the other leg is in the air. This is achieved by lateral rotation of the distal femur creating a waddling type gait. This is most noticeable in short-legged birds like ducks (Raikow 1985).

The fibula lies laterally and is short and not well developed in birds. The equivalent of the hock joint is between the tibiotarsus and the tarsometatarsus; movement here is mainly flexion and extension.

Tarsometatarsus

This is the fusion of tarsal bones 2, 3, and 4, to the corresponding metatarsal bones. The shape varies according to the locomotion of species. An elongated metatarsus conveys extra leverage for running or for takeoff in flight. The first metatarsus lies separate but is joined to the tarsometatarsus by ligaments. As it lies distally it can often be mistaken for a phalanx (Harcourt-Brown 1996; Raikow 1985; Smith & Smith 1997).

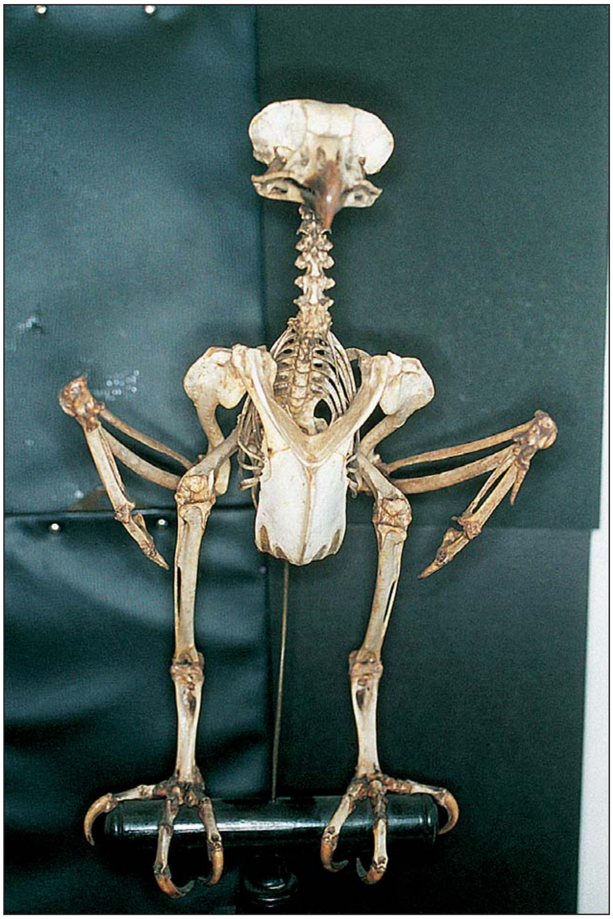


Figure 6.25 • Cranial view of skeleton of perching eagle owl (*Bubo bubo*).

Phalanges

Most birds have four digits with varying numbers of phalanges. Digit 1 will have two phalanges, digit 2 has three, digit 3 has four, etc. Digit 1 (the equivalent of our big toe) is often called the "hallux" and usually projects caudally. This is rudimentary in ground-dwelling birds and in fact the ostrich only has two toes (Bezuidenhout 1999; Evans 1996).

The main action of the digits is flexion and extension. When birds perch their tendons are flexed and small sprocket-like projections extend from these tendons and interdigitate to hold them in place. This reduces the amount of energy needed for perching.

CLINICAL NOTE

The gastrocnemius tendon runs caudally along tibial cartilage to insert on the plantar aspect of tarsometatarsus. Calcium deficiency leading to nutritional osteodystrophy causes malformation of the tarsometatarsus. This causes the tendons to slip medially, causing lameness and rendering the bird unable to perch properly.

Arrangement of digits

Birds are called digitigrade because, unlike humans, they actually walk on their toes and not on their feet. The arrangement of the digits depends on their function. Feet can be used to perch, grasp prey, wade, or become fully webbed for swimming.

Anisodactyl

The majority of birds (Columbiformes, Galliformes, Passeriformes, Falconiformes) have an adaptation for perching or holding prey such that they have one toe facing backward and three facing forward (Fig. 6.26). Passerines also have an extra extensor muscle, the extensor hallucis longis to extend their first digit. Galliformes commonly have spurs on the caudomedial aspect of the tarsometatarsus (Fig. 6.27); these are more developed in the male (King & McLelland 1984).

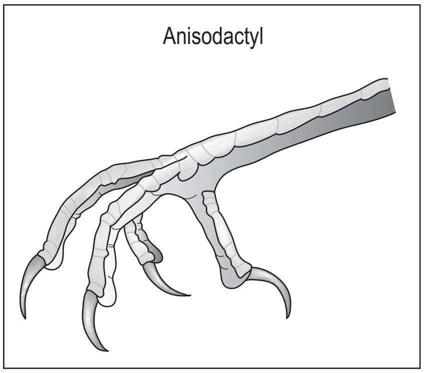


Figure 6.26 • Anisodactyl.
The majority of birds (e.g., passerines, pigeons) have one toe facing back and three facing forward. This is an adaptation for perching or holding prey.

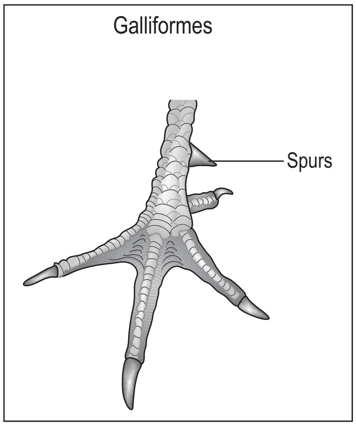


Figure 6.27 • Anisodactyl – Galliformes.
Galliforme foot showing spurs on the caudomedial aspect of the tarsometatarsus.

Zygodactyl

Species like psittacines, have two (first and fourth) toes facing caudally and two (second and third) facing cranially. These species use their feet for grasping and climbing (Fig. 6.28). Owls and ospreys have a basic zygodactyl foot but can move the fourth digit from back to front (Raikow 1985).

Palmate

This is seen in ducks, geese, swans, and gulls and is when the cranial digits 2, 3, and 4 are webbed. The capacity to grip is sacrificed and the backward-pointing digit loses contact with the ground (Fig. 6.29).

KEY POINTS

- Thin bone cortices with internal medullary struts for strength
- Hens deposit calcium in medullary cavity prior to laying
- Rigid fused backbone for stability during flight – many species have weak link around T4
- Flight muscles all located ventrally on sternum, nearer to bird's center of gravity
- Neck and tail most flexible parts of backbone
- Pelvis incomplete ventrally, with fossae for kidneys
- Primary feathers insert on manus while secondary feathers insert on caudal ulna

Celomic cavities

Birds have no diaphragm and so have one body cavity called the celom that extends from the first thoracic vertebra to the vent. This cavity is not lined by serosa, as in mammals, but instead contains 16 separate cavities, 8 of which are airsacs. The remaining eight cavities consist of three (two pleura and one pericardial) that resemble mammalian ones,

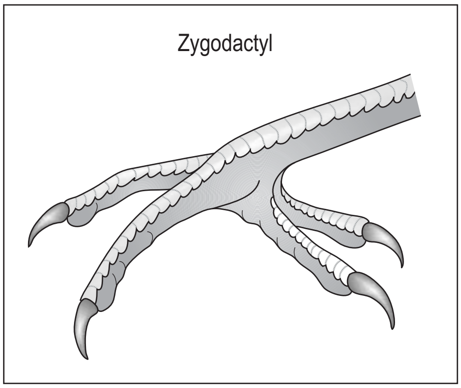


Figure 6.28 • Zygodactyl.
Psittacines have two toes facing caudally and two facing cranially. These feet are very dexterous and used for grasping food and climbing.

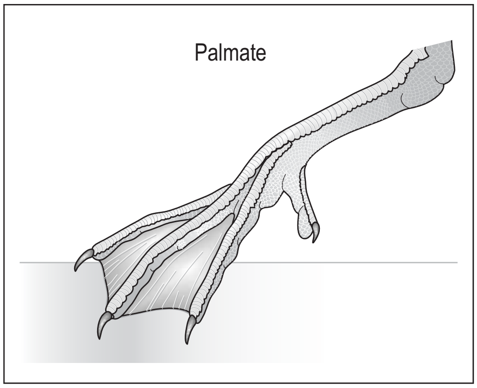


Figure 6.29 • Palmate.
Swimming birds like ducks, geese and gulls have webbing of the cranial digits II, III, and IV and are unable to grip.

and five peritoneal ones unique to birds. These cavities are of significance as they may influence the spread of pathology through the whole of the celomic cavity.

Pleural and pericardial cavities

The pericardial cavity is connected ventrally to the sternum and dorsally to the lung hilus and horizontal septum. The right and left pleural cavities are lined ventrally by a peritoneal sheet: the horizontal septum (Duncker 1979; King & McLelland 1975, 1984).

Peritoneal cavities

Birds lack an omentum, but a double-layered peritoneal sheet, the post-hepatic septum, stops the spread of disease by bringing in a healthy blood supply and divides the caudal cavity into three main parts. These are the middle intestinal cavity and two lateral hepatic cavities surrounding the liver. The hepatic cavities are in turn divided into the left and right ventral hepatic and left and right dorsal hepatic. The ventral hepatic ones are blind cavities between the ventral liver and body wall; the dorsal hepatic ones lie between the body wall and the dorsolateral liver. The intestinal cavity lies in the midline and contains the gastrointestinal tract, the gonads, and the oviduct, each of which lie suspended in their individual mesenteries (Duncker 1979; King & McLelland 1975, 1984).

CLINICAL NOTE

These cavities mean that egg peritonitis, for example, may be limited to the intestinal and left dorsal hepatic cavities only (King & McLelland 1984).

CARDIOVASCULAR SYSTEM

The heart lies in the midline and slightly to the right and is surrounded by a thin but tough pericardium (Akester 1984), which is attached to the dorsal surface of the sternum, the surrounding airsacs, and liver. The lungs lie dorsal to the heart and not surrounding it, while the liver lobes cover the base of the heart dorsally and laterally (Smith & Smith 1997).

The heart has four chambers with separate right and left sides so that oxygenated and deoxygenated blood never mix. It is quite similar to the mammalian heart except that in birds the ascending aorta curves to the right. In some species, like the chicken and ostrich, the cranial and caudal vena cavae enter first into a sinus venosus before entering the right atrium (King & McLelland 1984; Maina 1996; Rosenthal 1997b). Like reptiles, birds have a renal portal system.

The right atrioventricular valve is structurally unique to birds in that it has no chorda tendinae and forms only a thick, muscular flap of myocardium. The rest of the valves are more similar to mammalian ones, except the left atrioventricular valve is tricuspid (Akester 1984; Smith & Smith 1997). Unlike reptiles, where the muscle tissue of the atrium is continuous with the ventricle, birds have a specialized conducting system of Purkinje fibers which carry the impulse from the atrium to the ventricle. As in mammals, this begins at the sinoatrial node, located in the right atrium (Akester 1984; Smith & Smith 1997; West et al. 1981).

Arterial system

The aortic arch curves to the right and gives rise almost immediately to two very large brachiocephalic trunks which are responsible for distributing about three quarters of the cardiac output to the wings, pectoral muscles, and head (Akester 1971; West et al. 1981). These soon branch into the subclavian arteries, which supply the wings (brachial artery) and flight muscle (pectoral artery), and the carotid arteries which supply the head (Fig. 6.32). The carotid arteries run along a groove at the base of the cervical vertebrae close to the axis of rotation. This prevents movements of the flexible neck arresting blood flow to the brain (King & McLelland 1984; Rosenthal 1997b; Smith & Smith 1997).

CLINICAL NOTE

Unlike mammals, the heart is obscured at its base by liver lobes rather than the lungs. This gives an hourglass appearance to the cardiac and hepatic shadow on ventrodorsal radiographs in many psittacine species (Figs. 6.30 and 6.31). However, macaws have a relatively small liver, which might lead to an over diagnosis of cardiomegaly (Smith & Smith 1997).

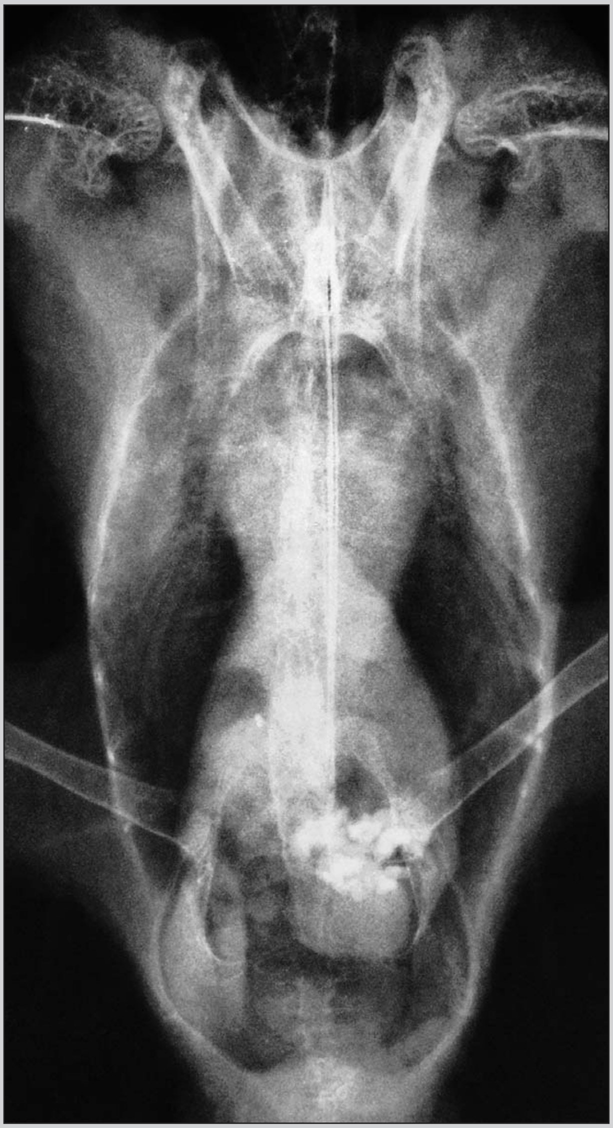


Figure 6.30 • Ventrodorsal radiograph showing normal cardiac and hepatic silhouette in a cockatiel (*Nymphicus hollandicus*). Grit is visible in the gizzard which lies at the level of the acetabuli.

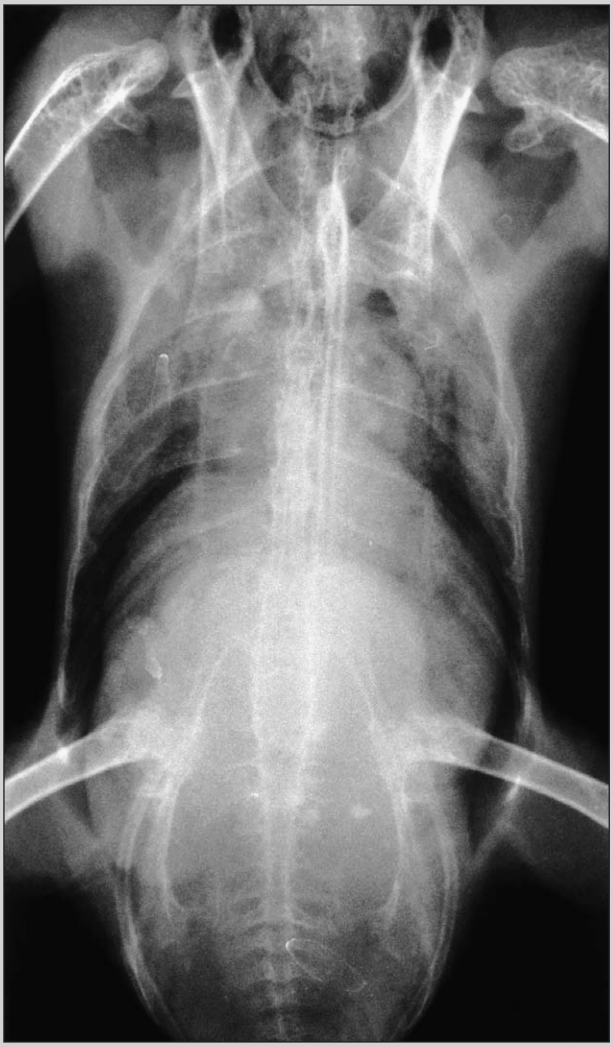


Figure 6.31 • Radiograph showing hepatomegaly secondary to lymphoma in an African gray parrot (*Psittacus erithacus*).

CLINICAL NOTE

The large brachiocephalic trunks can often be seen end on in ventrodorsal radiographs of large birds and must not be confused with fungal granulomas (Smith & Smith 1997).

The pelvic limb is supplied by the external iliac artery and the ischiatic artery that meets the femoral artery at the stifle to form the popliteal artery. It is this artery that forms an arteriovenous network of vessels (*rete mirabile*) in many wading birds. This aids in heat exchange by warming cold blood from the extremities (Smith & Smith 1997).

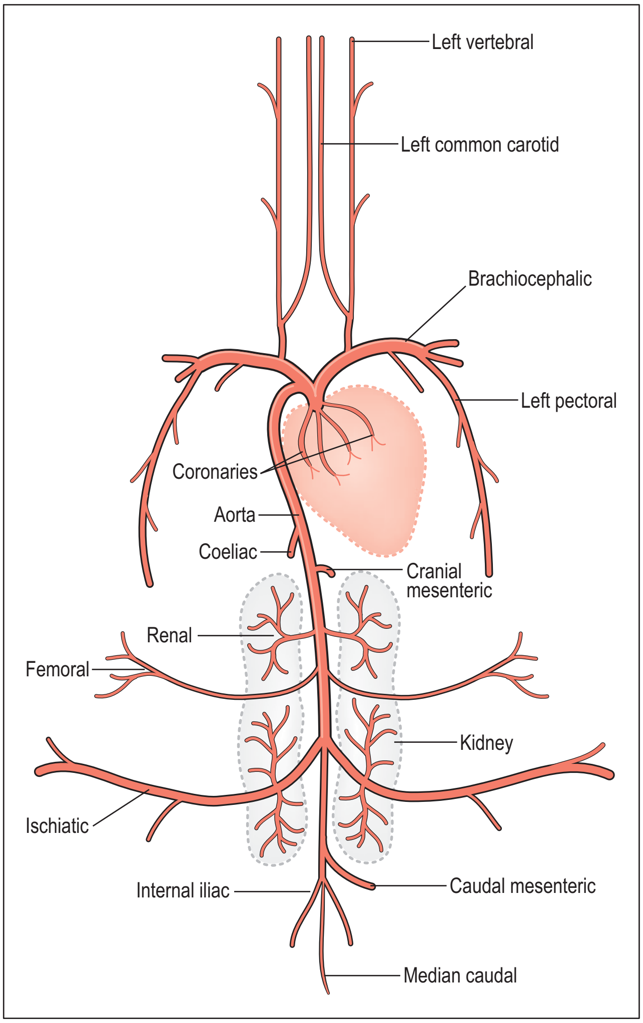

Left vertebral
Left common carotid
Brachiocephalic
Left pectoral
Coronaries
Aorta
Coeliac
Cranial mesenteric
Renal
Femoral
Kidney
Ischiatic
Internal iliac
Caudal mesenteric
Median caudal

Figure 6.32 • The major systemic arteries in the bird.

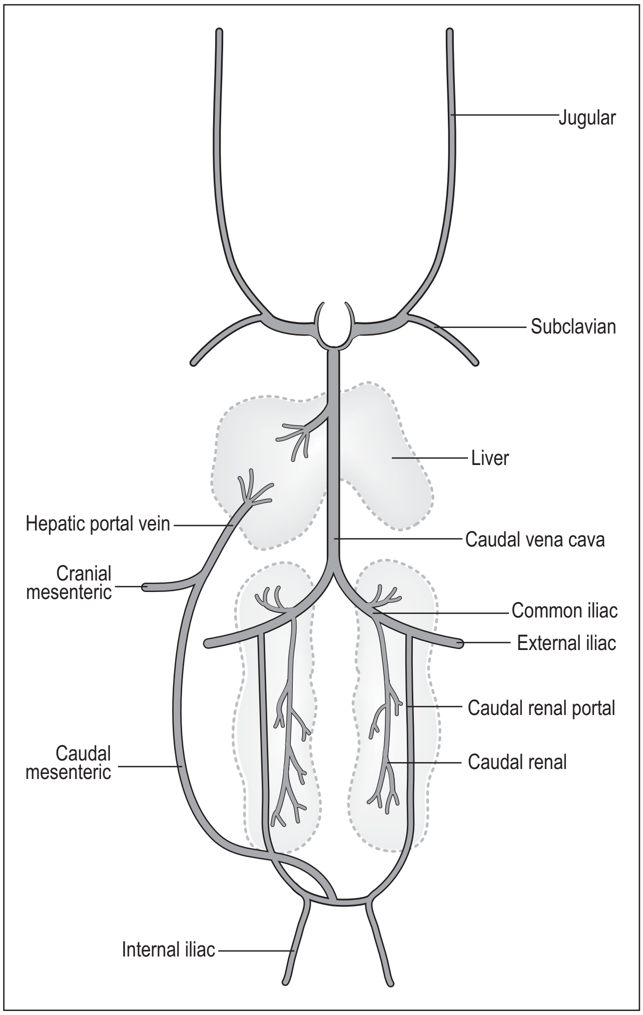

Jugular
Subclavian
Liver
Hepatic portal vein
Caudal vena cava
Cranial mesenteric
Common iliac
External iliac
Caudal renal portal
Caudal mesenteric
Caudal renal
Internal iliac

Figure 6.33 • The major systemic veins of birds.

Venous system

The cranial vena cavae are paired and receive blood from the neck and head via the jugulars, and from the wing and breast via the subclavian veins. At the angle of the jaw there is a transverse anastomosis between the two jugulars which allows blood to bypass from one side to another in case one vein gets compressed during neck movement. This anastomosis slopes caudally towards the right jugular and this may explain why, in most species, the right jugular is much larger than the left (Akester 1971; West et al. 1981). In some small cage birds the left jugular is lost altogether (Evans 1996; King & McLelland 1984).

Venous blood from the pelvic limbs, lower body, and hindgut enters the renal portal system, which then joins the caudal vena cava. The main bulk of the gastrointestinal tract, pancreas, and spleen drains into the hepatic portal vein and the liver. Unique to birds is the large caudal mesenteric or *coccygeal mesenteric vein*, which drains the hindgut mesentery and connects the hepatic portal vein to the renal portal vein. As blood can flow along this vein in both directions flow can be switched between the kidneys and the liver (Akester 1971) (Fig. 6.33).

Renal portal system

In birds, venous return from the pelvic limbs goes through the kidneys before reaching the caudal vena cava, contributing about two thirds of renal flow (Smith & Smith 1997). This is controlled by portal valves at the junction of the common iliac and renal veins (Akester 1971; West et al. 1981). These are unique in that they contain innervated smooth muscles. Normally, these valves are closed to direct blood through the kidney where they take part in tubular secretion (see Urinary system). In times of stress adrenaline opens these valves to allow the blood to bypass the kidneys completely. It can then take a short cut via the coccygeal mesenteric vein to the liver or directly into the caudal vena cava to the heart (Akester 1971, 1982; Smith & Smith 1997; West et al. 1981).

Venepuncture sites

(See Echols 1999.)

Three large peripheral veins are suitable for avian blood sampling:

- The deep ulnar vein (basilic) – This becomes cutaneous at the elbow on the ventral aspect of the wing. Hematoma formation is always a problem so digital pressure must be applied immediately post sampling.
- Right jugular vein – This is the least prone to extravasation post sampling. The vein lies in a natural featherless tract (aptyeria) so can be easily visualized in most birds. However, Columbiformes and Anseriformes lack apteria, making visualization more difficult (Echolls 1999) (Fig. 6.34).
- Medial metatarsal – This is less likely to form a hematoma, owing to the scales of the leg. It is a useful venipuncture site in waterfowl, although feathering on the leg and the thick skin can make this vessel harder to identify.
- Toe-nail clipping – Small samples can also be taken by this method but it can be painful and the nail must be cleaned well to avoid contamination from urates.

Cardiac physiology

In order to be able to fly birds have high oxygen demands, so consequently the avian heart is 50 to 100% larger than in mammals of the same size (Maina 1996; Rosenthal 1997b; Smith & Smith 1997). The size of the heart also depends on the amount of aerobic energy each species expends. For example, a large bird like a swan will have a proportionately smaller heart for its size than a racing pigeon (Maina 1996; Smith & Smith 1997). Birds also have a far greater exercise capacity than humans: at maximum exercise, the cardiac output in a flying budgie is seven times greater than that of a man or dog (King & King 1979; King & McLelland 1984; Maina 1996).

In order to pump large volumes of blood to the wings, head, and flight muscles, birds have a much higher cardiac output than mammals. This is achieved by a high stroke volume, fast heart rates (150–350 resting), and slightly lower peripheral resistance. They also have stiffer arteries to improve blood flow and maintain a high blood pressure, ranging from 108–250 mmHg (compared to an average of 150 mmHg in humans). Turkeys have the highest pressure of all vertebrates, being as high as 350 mmHg (Akester 1984; Maina 1996). The consequences of this high pressure can, however, mean that aortic rupture, heart failure and hemorrhage are a common cause of death in stressed avian patients (Rosenthal 1997b; Welty 1982b).

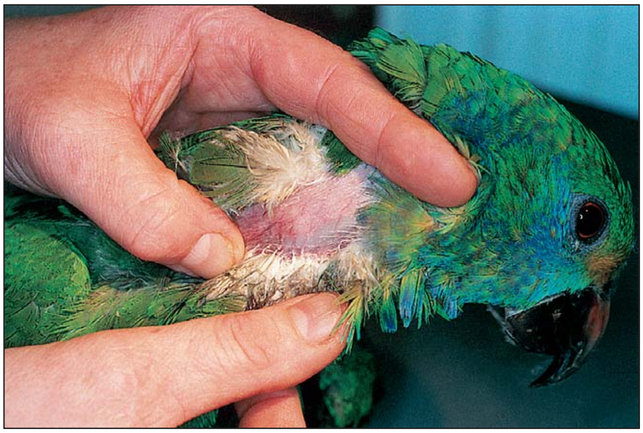


Figure 6.34 • Blood sampling from the right jugular vein of an Amazon parrot.

GENERAL INTEREST

The hummingbird has the largest heart of all, relative to its size, in order to sustain the aerobic demand of hovering. In contrast to the mouse (where the heart accounts for 0.5% of its body mass) its heart represents 2.4%. When hovering it can reach a heart rate of over 1000 beats per minute (King & McLelland 1984).

CLINICAL NOTE

Grossly, the major avian arteries appear white due to the collagen fibers of the tunica adventitia. These fibers produce the stiff arteries that help combat the high blood pressure and improve blood flow. The downside of this is that birds are susceptible to atherosclerosis of the aorta and brachiocephalic trunk. This is commonly seen in aged Amazon parrots (Rosenthal 1997b).

Diving birds

Unlike reptiles, birds cannot shunt blood away from the lungs while diving because the ventricles are completely divided. Instead, diving birds use selective vasoconstriction, bradycardia, and a drop in cardiac output. Blood flow is diverted from the skin, muscles and gastrointestinal tract to the brain, sensory organs, and myocardium to protect them from hypoxia during a dive (Akester 1984; Fowler 1986; Rosenthal 1997b).

Blood components

Blood volume varies from 5 to 13% of body mass. The blood cells are made up of nucleated erythrocytes, thrombocytes, lymphocytes, monocytes, heterophils, eosinophils, and basophils.

Erythrocytes

The avian erythrocytes are oval in shape and, being nucleated, are usually larger than those in mammals (Fig. 6.35). Flightless birds like the ostrich have the largest erythrocytes whereas the more higher evolved good fliers, like passerines, tend to have smaller erythrocytes (Maina 1996; Welty 1982b). Small erythrocytes produce a greater combined surface area and more efficient gas exchange, thus allowing for higher oxygen absorption and hence a metabolic rate that is 10 times that of mammals (Hodges 1979; King & McLelland 1984).

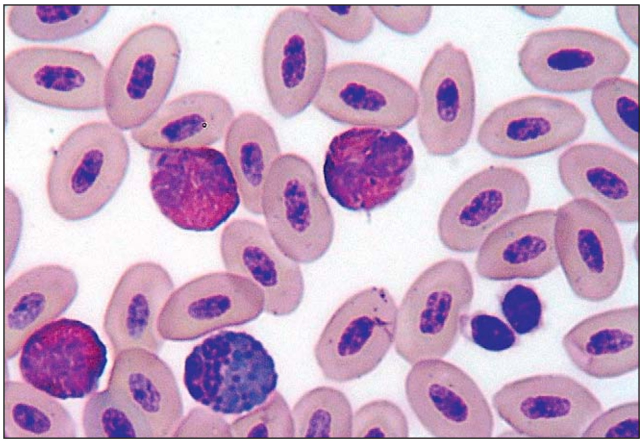


Figure 6.35 • Blood smear from an African gray showing nucleated avian erythrocytes; three heterophils, one eosinophil and two thrombocytes.

The avian erythrocyte does not necessarily contain more hemoglobin than mammals but species that fly at high altitudes have a higher hemoglobin affinity (Butler & Bishop 2000; Welty 1982b).

CLINICAL NOTE

EDTA causes lysis of red blood cells in certain species, like the ostrich, crow, and crane. Avian leukocytes are very fragile so particular care must be taken when blood smears are made. The use of cover slip smears may avoid cell disruption. Smears should be made immediately after collection because blood coagulation takes place faster in birds (30–60 s) than in mammals.

GENERAL INTEREST

The ability to absorb more oxygen means that birds can fly at high altitudes. The Bar-headed goose (*Anser indicus*) migrates over Mount Everest and the Himalayas and has the amazing ability to fly from sea level to an altitude of 9200 m without having to acclimatize (King & King 1979; Scheid & Piiper 1972).

Control of erythropoiesis

Erythropoiesis takes place in the bone marrow. The avian erythrocyte has a short life span compared to that in mammals, presumably due to their high metabolic rate and body temperature. For example, duck and pigeon erythrocytes last 42 and 35–45 days, respectively, compared to 90–120 and 45–50 days in humans and rats (Freeman 1971; Maina 1996). This short life span means that persistent anemias should be investigated thoroughly.

Blood loss

Birds (especially flying ones) are better able to tolerate blood loss than mammals, with the pigeon being able to lose 8% of its body mass from hemorrhage. This rapid restoration of blood volume may be due to pronounced vasoconstriction in skeletal muscles raising the blood pressure and to large capillary beds that ensure rapid absorption of tissue fluid (Smith & Smith 1997).

Thrombocytes

Thrombocytes are fragile, nucleated cells analogous to the mammalian platelet, although they originate from a stem cell and not from megakaryocytes like platelets (Freeman 1971; Powers 2000). Although avian thrombocytes are involved in the clotting process they have little thromboplastin and so do not appear to trigger the intrinsic clotting process (Archer 1971; Hodges 1979; Powers 2000). Instead, unlike mammals, it is the extrinsic thromboplastin shed by the damaged tissue that plays a more major role in clotting. This reliance on extrinsic clotting pathways may exist to prevent exsanguination in animals with such high blood pressure and rapid heart rates (Powers 2000).

Lymphocytes

T lymphocytes are produced by the thymus. They have a long life span and develop cellular immunity. B lymphocytes produced by the Bursa of Fabricius are involved with humoral cell responses and have a short life span.

Monocytes

These are rarely seen in peripheral blood smears, so low or zero counts are common. They can be elevated with chronic infections like psittacosis, tuberculosis, and mycotic infections.

Heterophils and eosinophils

Heterophils are similar to mammalian neutrophils, having a polymorphic nucleus. They are the equivalent of neutrophils but stain acidophilic (Hodges 1979). Eosinophils account for about 2% of total leukocytes (Freeman 1971); their function is uncertain but may be associated with tissue damage or parasitic disease.

KEY POINTS

- Avian heart is larger for body size than mammals
- Aorta arches to the right in birds. Brachiocephalic vessels are very large as they supply pectoral arteries for flight
- Heart and liver form an hourglass appearance on ventrodorsal radiographs in many psittacines
- Renal portal vein
- Nucleated erythrocytes
- Higher blood pressure means greater tendency to hemorrhage, although birds are surprisingly tolerant of blood loss
- EDTA lyses red blood cells in some species so a fresh blood smear is always advisable

IMMUNE SYSTEM

Birds have both primary and secondary lymphoid organs. The primary organs are the Bursa of Fabricius and the thymus; the secondary ones are the spleen, intestinal lymphoid tissue and bone marrow (Rose 1981; Schmidt 1997).

Thymus

The thymus is found in the neck and consists of three to eight flattened, pale pink lobes lying along the neck, close to the jugular vein. In most birds some tissue persists throughout life although it decreases in size at sexual maturity (Payne 1984; Schmidt 1997). T-lymphocyte precursors are produced by stem cells in the embryo yolk sac and bone marrow and then develop into T lymphocytes in the thymus. These act in cell-mediated immunity, such as delayed hypersensitivity reactions (Rose 1981; Payne 1984).

Bursa of Fabricius

The Bursa of Fabricius is unique to birds. It was first described in the hen by Hieronymus Fabricius in 1621 (Payne 1984). It is a dorsal diverticulum in the proctodeum, which contains folds of lymphoid tissue. In psittacines, galliformes and passerines the bursa is oval or pear shaped, with a central cavity. It has a thick wall in the domestic fowl but is thin and saclike in the psittacines and passerines (King & McLelland 1984; Schmidt 1997). It reaches maximum size before sexual maturity and begins to involute at about 2–3 months. Involution is slower in geese, which do not reach sexual maturity until 2 years of age.

Stem cells in the yolk sac produce B-lymphocyte precursors, which then develop in the bursa. The bursa then seeds other lymphoid organs with B-lymphocytes and is also necessary for normal thymal development. The bursa and dependent lymphoid tissue produce antibodies that are the main defense against invading microorganisms (Schmidt 1997).

CLINICAL NOTE

In ratites the bursa and proctodeum form a single large cavity which has often been mistaken for a urinary bladder (King, AS 1981a; King & McLelland 1984).

Lymphatic system

Lymphatic vessels are less numerous than in mammals and usually follow the blood vessels closely (Rose 1981; Payne 1984). Most species have paired thoracic ducts on either side of the spine that drain the lymph from the hind- limb and abdominal vessels and deliver it into the jugular veins at the base of the neck.

Lymphoid nodules are scattered throughout the digestive tract but especially in the oropharynx, the ceca (called "cecal tonsils"), and small intestine (Payne 1984; Schmidt 1997).

CLINICAL NOTE

Birds do not have lymph nodes, except for ducks and geese, which have two primitive pairs: a cervicothoracic pair near the thyroid gland and a lumbar pair near the kidneys (Rose 1981; King & McLelland 1984; Payne 1984).

Spleen

The brownish red spleen lies to the right of the celom between the proventriculus and ventriculus. It phagocytoses aged erythrocytes, and aids in lymphopoiesis and in the production of antibodies. It does not form a significant blood reservoir, as in mammals, so is relatively small in birds (Rose 1981; Schmidt 1997). It can vary in shape from oval in pigeons and chickens, to triangular in ducks and geese, to elongated in the budgie (Dyce et al. 2002; King & McLelland 1984; Schmidt 1997).

KEY POINTS

- No lymph nodes
- Bursa of Fabricius found in immature birds
- Spleen does not act as a blood reservoir as in mammals

RESPIRATORY SYSTEM

Birds use their respiratory system not only for gaseous exchange but also for vocalization and thermoregulation.

The avian respiratory system is unique in that the lungs are small, undergo little change in volume when breathing, and have airsacs that act as bellows but do not participate in gas exchange. This segregation of ventilation and gas exchange helps to increase the total gas exchange surface area. The bellows system allows continuous gas flow as opposed to the "in and out" tidal flow of mammals. The net result is that in birds up to 10 times more oxygen can be absorbed.

Birds have no diaphragm, instead the horizontal septum separates the lungs from the viscera. This septum plays no active role in respiration but passively helps to displace the viscera during breathing.

Nasal cavity

Birds can breathe through their nose or mouth (Powell 2000). The nasal cavity is compressed laterally and divided medially by a very thin septum. The nasal openings or "nares" lie laterally at the base of the beak, where they can be surrounded in species like psittacines by a thick cere. Many species also have a hard, keratinized structure called the *operculum* at the center of each nare that acts as a baffle to prevent inhalation of foreign bodies. Air enters through these nares into the conchae of the nasal cavity, passes down through the slitlike choana and across the oropharynx to the glottis (King & McLelland 1984).

CLINICAL NOTE

Some birds, like gannets and boobies, have no external nares but breathe through a narrow gap between the distal upper and lower beak. This enables them to dive at high speed without water blowing out of their nostrils (Fig. 6.36).

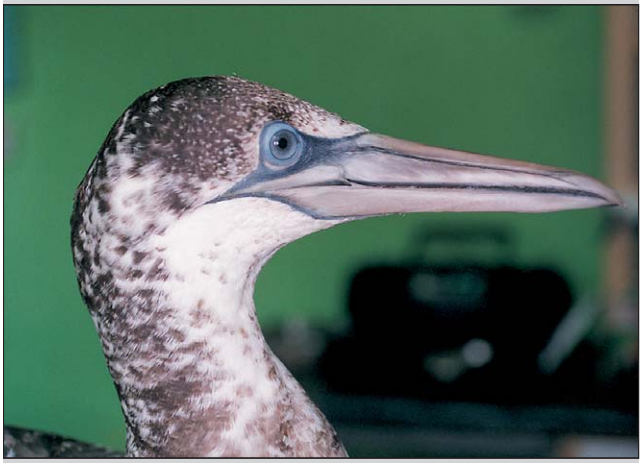


Figure 6.36 • Juvenile gannet (*Sula bassana*) showing lack of external nares.

Nasal conchae

The conchae are highly vascular, epithelial folds in the nasal cavity that increase the surface area over which air flows, allowing it to be filtered and warmed. They are divided into rostral, middle, and caudal parts and play a major role in olfaction, filtering, and thermoregulation (King & McLelland 1984).

Olfactory epithelium in the caudal conchae picks up scent particles, ciliated epithelium filters out foreign particles, and mucus secreted by goblet cells flushes these through the choana into the oropharynx. An extensive network of blood vessels, the rete mirabile, helps control the water and heat loss by warming or cooling air entering the nasal cavity. This helps prevent excessive water loss and is particularly important in desert and migrating birds.

Infraorbital sinus

This paranasal sinus is particularly well developed in psittacines and becomes superficial ventromedial to the orbit (Fig. 6.37). It has numerous diverticula, which extend into the premaxilla, around the ear and rostral orbit, and into the lower beak. It communicates dorsally with the caudal and middle conchae and also with the cervicocephalic airsac at its caudal extent. In some birds (Psittaciformes and Anseriformes) the right and left sinuses communicate.

CLINICAL NOTE

Nebulization is an excellent way of rehydrating an avian patient and helps compensate for any evaporative water loss due to respiratory problems.

Nasal gland

The nasal or salt gland lies just dorsal to the orbit and opens into the nasal cavity at the level of the rostral concha from where saline is then sneezed from the nostrils. It secretes a hypertonic solution enabling seabirds to drink seawater. The gland is similar to the kidney and has a countercurrent blood supply which removes sodium ions from the bloodstream (King & McLelland 1984).

Larynx

The laryngeal opening (or rima glottis) is slitlike and, unlike in mammmals, is not covered by an epiglottis (Fig. 6.51). It is usually found at the back of the tongue but is often

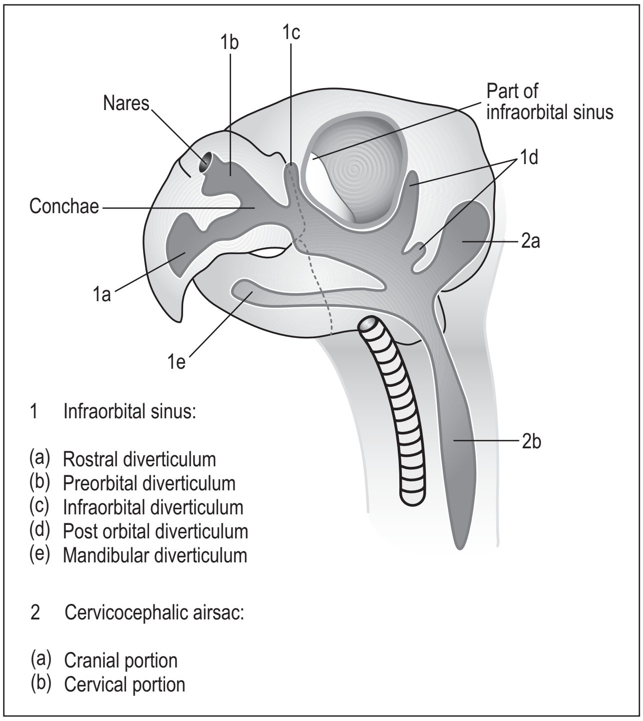

1b
1c
Nares
Part of infraorbital sinus
1d
Conchae
2a
1a
1e
2b
1 Infraorbital sinus:
(a) Rostral diverticulum
(b) Preorbital diverticulum
(c) Infraorbital diverticulum
(d) Post orbital diverticulum
(e) Mandibular diverticulum
2 Cervicocephalic airsac:
(a) Cranial portion
(b) Cervical portion

Figure 6.37 • Psittacine skull showing infraorbital sinus which is particularly well developed in these species.

CLINICAL NOTE

In psittacines the free communication between the nasal cavity, infraorbital cavity, skull, and airsacs makes the treatment and drainage of sinus infections very difficult. Often the first signs of infection can be swellings rostral and ventral to the eye where the infraorbital sinus lies superficially just under the skin and subcutaneous tissues (Fig. 6.38).

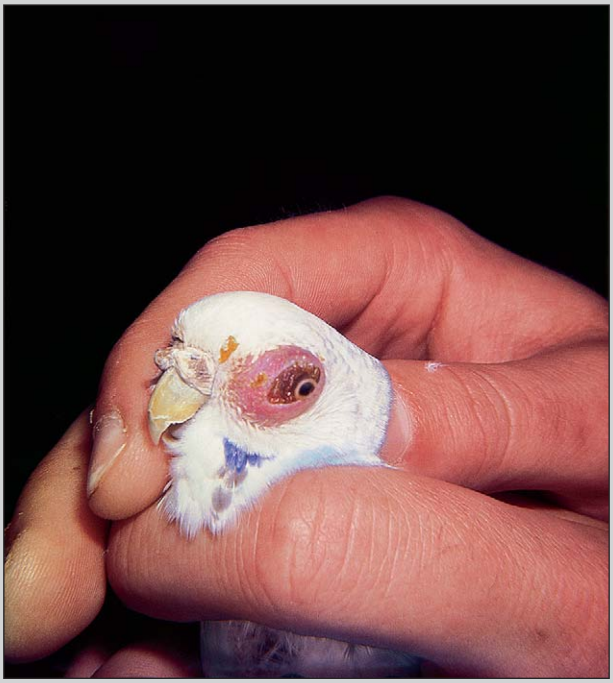


Figure 6.38 • Swelling of the infraorbital sinus in psittacines is a symptom of sinusitis and not an ocular problem.

obscured by the fleshy tongue in psittacines. There is no soft palate but the rima glottis regulates the passage of air by a dilator and constrictor muscle that prevents aspiration of food material. The larynx plays no role in sound production (King & McLelland 1984).

Trachea

The trachea is composed of rigid interlocking rings and is relatively long, given birds' size. This is because birds need long necks to help manipulate objects with their beaks. The greater air resistance created by elongation means the diameter of the rima glottis and trachea is wider to compensate (Hinds & Calder 1971).

In some species the trachea is so long it forms coils; in the Trumpeter swan these lie in a cavity of the sternum. Toucans and mynahs have a normal ventral deviation of the trachea just cranial to the thoracic inlet. In penguins, a median septum divides it into left and right tubes, making it very easy to intubate a primary bronchus by mistake (King & McLelland 1984; Powell 2000).

To compensate for the increased tracheal length, birds minimize air resistance by having a trachea of wider diameter than mammals of equivalent size. Birds with tracheal convolutions and greater lengths also have wider diameters to increase total volume. However, this results in birds having a dead space 4.5 times that of mammals (Hinds & Calder 1971). To overcome this birds have increased tidal volume and (relative to size) a slower and deeper rate of breathing (Hinds & Calder 1971). For example, a mammal of 100 g would have a resting respiration rate of 100 breaths per minute while in a bird of equivalent size it would be 30 per minute (Welty 1982b). Birds with long necks, like swans, breathe as slowly as 10 breaths per minute and the ostrich has the slowest rate of all birds at 3 to 5 breaths per minute (Brackenbury 1987).

Syrinx

The *syrinx* (Greek word for panpipe) is the bird's voice box and is analogous to the mammalian larynx except that it lacks vocal cords which vibrate with air currents. It is rudimentary in species like vultures and ostriches (King, AS 1989).

The syrinx can be classified as tracheal, tracheobronchial or bronchial depending on location. The most common type is the tracheobronchial (Fig. 6.39), located at the bifurcation of the trachea, and has a median cartilage called the *pessulus*, at the bifurcation. This type is found in psittacines although they lack a median pessulus.

The syrinx consists of a series of modified tracheobronchial cartilages, two vibrating tympaniform membranes and muscles which vary the membrane tension. These thin membranes line the medial and lateral bronchi and sound is produced during expiration by vibration of air through the

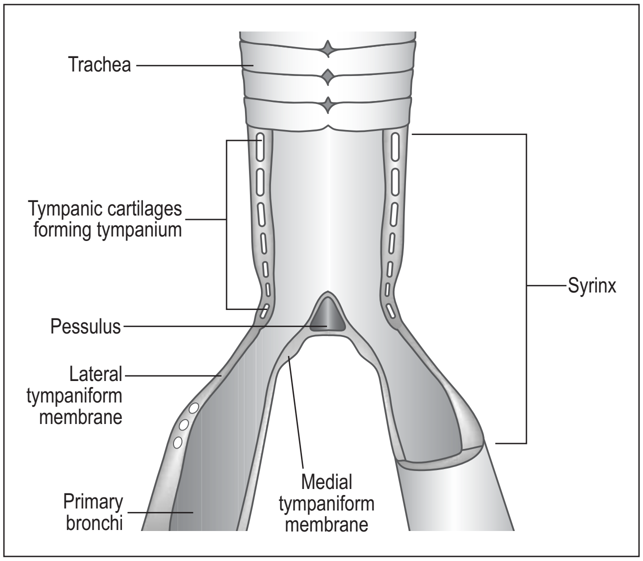

Trachea
Tympanic cartilages forming tympanium
Syrinx
Pessulus
Lateral tympaniform membrane
Primary bronchi
Medial tympaniform membrane

Figure 6.39 • Longitudinal section of tracheobronchial syrinx showing tympaniform membranes and syringeal cartilages.

syrinx (King, AS 1989; King & Molony 1971). The surrounding interclavicular airsac gives the voice resonance by pushing against these membranes. Birds with long coiled tracheas have deep resonant voices, hence the call of the Trumpeter swan (Gaunt 1987).

The number of syringeal muscles varies with species. Despite their great speaking ability parrots have a relatively simple syringeal apparatus with only three pairs of syringeal muscles (Evans 1996; Welty 1982b). Hawks have only one pair while the songbirds have five pairs (King, AS 1989). In many songbirds the two sides of the syrinx are independently controlled allowing them, literally, to sing a duet with themselves (Gaunt 1987; King & McLelland 1984).

CLINICAL NOTE

As the trachea is narrowed at the site of the syrinx this is a common site of obstruction by foreign bodies like seeds or fungal granulomas. Birds exhibiting voice changes should have the syrinx examined endoscopically. Other common causes of voice changes can be goiter pressing on the syrinx or damage to the surrounding interclavicular airsac.

CLINICAL NOTE

Male ducks have modified their tracheal syrinx into an osseous bulla to give their voice resonance. This can be seen radiographically near the left side of the thoracic inlet on the ventrodorsal view and can be used in sexual differentiation in monomorphic species (Dyce et al. 2002; King, AS 1989).

Lungs

The avian lungs are far more rigid than mammalian lungs because they contain more cartilage and are thus less compressible. They are small, compact and spongy and, being quite dense, occupy less space than mammalian lungs. They are bright pink in color and closely adherent to the rib cage dorsally, which leaves furrow marks on the surface. Ventrally they are lined by the horizontal septum. Due to the absence of a diaphragm the lungs do not collapse if the celom is entered via surgery or endoscopy (Fig. 6.40).

Bronchi

Each primary bronchus runs through the whole length of the lungs (where they are called *mesobronchi*) and terminates in the caudal airsacs. On entering the lungs each bronchus then gives rise to four sets of secondary bronchi named according to the area of the lung they supply: mediodorsal, medioventral, laterodorsal, and lateroventral (Fig. 6.44). These terminate in tertiary bronchi called *parabronchi* where blood gas exchange takes place. All bronchi

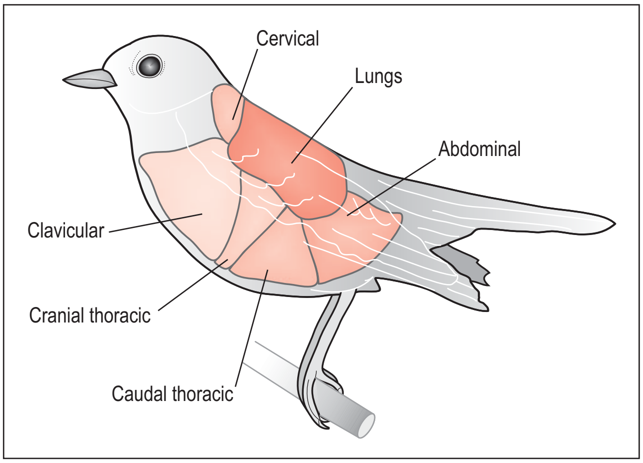


Figure 6.40 • Location of avian lungs and airsacs.

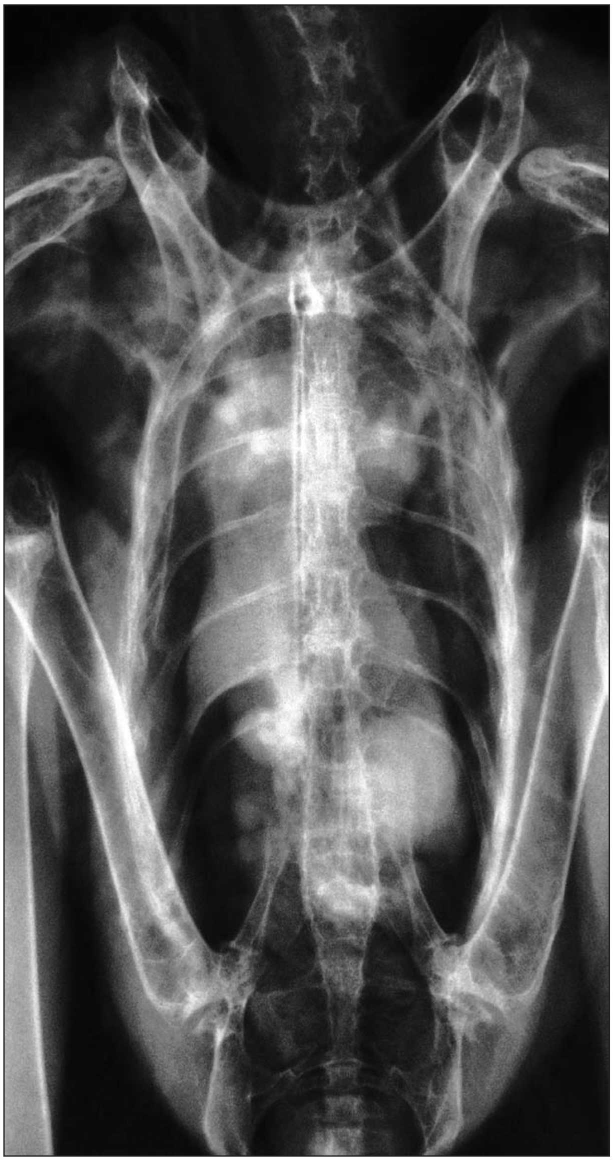


Figure 6.41 • Ventrodorsal radiograph of lungs and airsacs in a normal bird of prey.

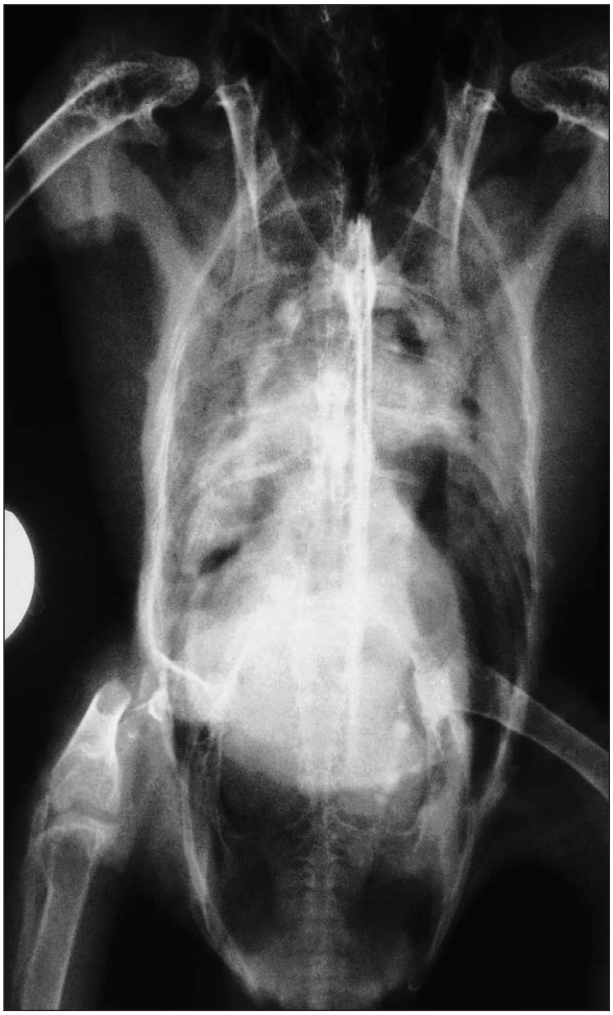


Figure 6.42 • Ventrodorsal radiographs of lungs and airsacs in a parrot attacked by a dog, showing fractured femur and hemorrhage in the thoracic airsacs.

CLINICAL NOTE

During anesthetics tidal volume may be reduced by as much as half when the bird is lying on its back. This is due to compression of the viscera on the caudal air sacs (King & Payne 1964) (Fig. 6.43). The absence of a diaphragm also means that, when anesthetized, birds may not breathe regularly, owing to the lack of sternal muscle contraction. Ventilation by positive pressure ventilation is always recommended (Fedde 1993).

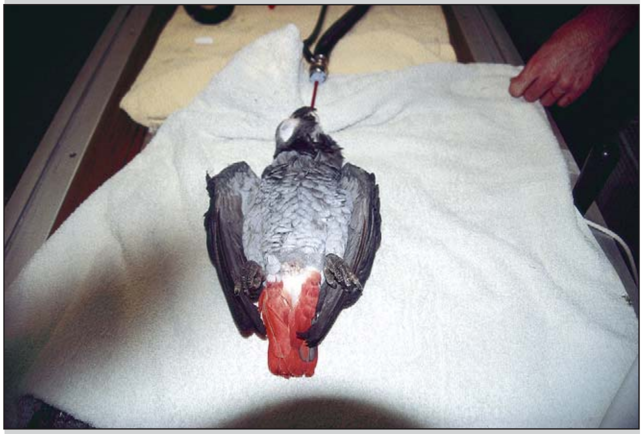


Figure 6.43 • Prolonged dorsal recumbency should be avoided during general anesthetics due to mass of the viscera compressing caudal airsacs.

CLINICAL NOTE

On lateral radiographs the tertiary parabronchi are seen end on and this gives a honeycomb appearance to the lung (Fig. 6.54). Absence of this normal appearance can indicate pathology (Smith & Smith 1997).

are lined by smooth muscle causing dilation and contraction (Lasiewski 1972).

Parabronchi

The parabronchi, which can be seen by the naked eye, make up the bulk of the lung tissue. They have invaginations called *atria* which lead to a labyrinth of microscopic air capillaries extending out to perform gas exchange (Fig. 6.45). These lie in close proximity to tiny blood capillaries, giving the lung a highly vascular appearance. The air capillaries are lined by surfactant, which keeps small cavities open by lowering surface tension. If this is not present, surface tension at the air–blood interface will collapse the capillaries leading to build up of transudate fluid (Lasiewski 1972; Powell 2000).

The number of these tertiary parabronchi increases with active flight; for example ducks have approximately 1800 whereas the flightless domestic fowl (*Gallus gallus*) has only 300 to 500 (Scheid & Piiper 1987).

Most of these parabronchi are a parallel series of hundreds of tubes called *paleopulmonic* bronchi. In most birds* there are also irregular branched parabronchi ("neopulmonic bronchi"), which never comprise more than 25% of the parabronchi (Maina 1996; Powell 2000; Scheid & Piiper 1987). Air flow through the paleopulmonic is always in the same direction during inspiration and expiration; however, in the neopulmonic bronchi it is bi-directional according to the phase of breathing. As no airway valves have been found it is thought that the shape and alignment of the secondary bronchi creates a pressure differential between the cranial and caudal airsacs influencing air flow through the parabronchi (Brackenbury 1987; McLelland & Molony 1983; Scheid & Piiper 1971).

*Some more primitive birds, like the kiwi, penguin, and emu have only paleopulmonic bronchi and these do have bi-directional flow (Fedde 1993; King & McLelland 1984).

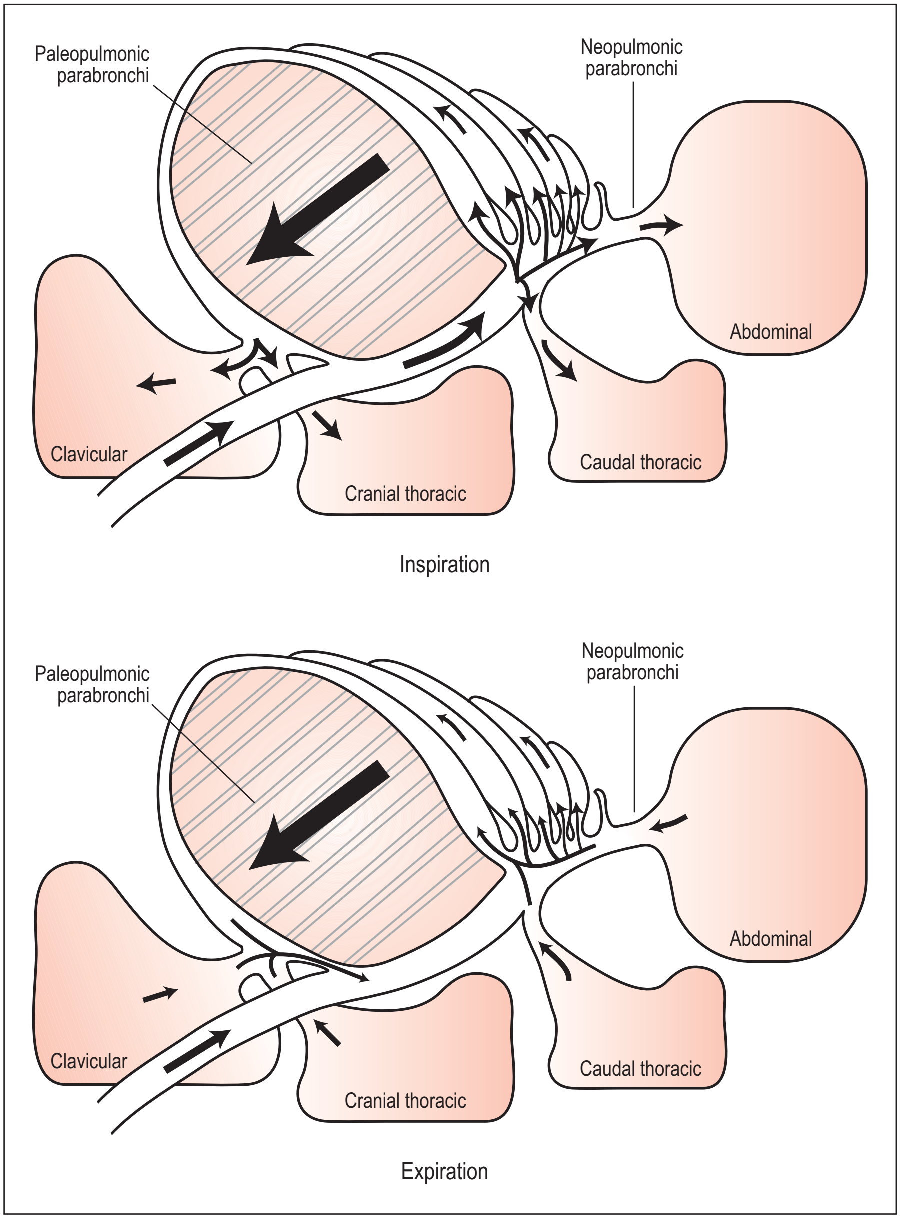

Paleopulmonic parabronchi
Neopulmonic parabronchi
Abdominal
Clavicular
Cranial thoracic
Caudal thoracic
Inspiration
Paleopulmonic parabronchi
Neopulmonic parabronchi
Abdominal
Clavicular
Cranial thoracic
Caudal thoracic
Expiration

Figure 6.44 • Diagram showing air flow through the respiratory tract of birds during inspiration and expiration. Air flows in the same direction from caudal to cranial in both phases of respiration.

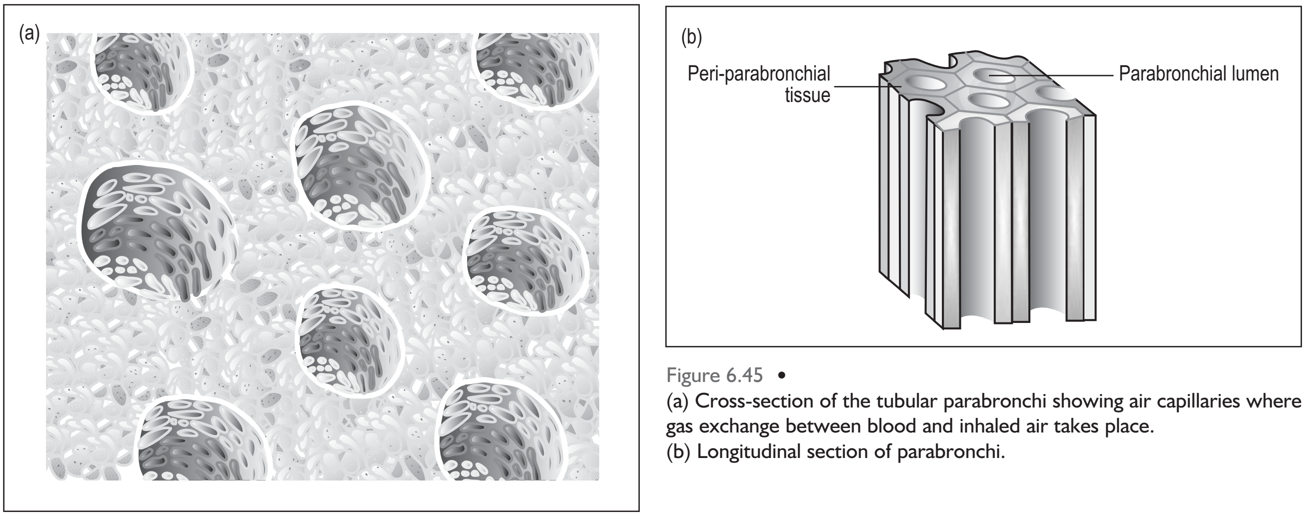

(a)
(b)
Peri-parabronchial tissue
Parabronchial lumen

Figure 6.45 •
(a) Cross-section of the tubular parabronchi showing air capillaries where gas exchange between blood and inhaled air takes place.
(b) Longitudinal section of parabronchi.

Gaseous exchange

Flight and the ability to fly at altitude means that birds have much higher oxygen demands than mammals. Avian lungs are 10 times more efficient than mammalian lungs in capturing oxygen due to the following modifications:

Thin blood–gas barrier

The air capillaries of the lung (equivalent to the mammalian alveoli) are finer and more numerous and the blood–gas barrier is very thin (Evans 1996; King & Molony 1971; Scheid & Piiper 1972). In fact, the capillaries are so narrow it is said the erythrocytes have to line up in single file! This is possible because, unlike mammalian lungs which have to expand and contract with every breath, the fixed avian lungs require little interstitial tissue for added strength. Stronger fliers like the passerines have a thinner blood–gas barrier than flightless birds such as chickens (Maina 1989; McLelland & Molony 1983).

Cross-current blood flow

The blood flow is at right angles to the airflow, giving a cross-current exchange system. This means that blood flow is always at right angles no matter which way the air is flowing (Scheid & Piiper 1972, 1987). Cross-current exchange allows more efficient absorption of oxygen without incurring high levels of carbon dioxide in the blood (Fedde 1993; Maina 1989; McLelland & Molony 1983).

One way airflow

The airflow through the lungs is unidirectional as opposed to the “in and out” tidal flow of mammals (Scheid & Piiper 1972) (Fig. 6.46). The parabronchi, being tubes and not dead-end sacs like alveoli, allow for continuous gas exchange in the avian lung and this may explain why birds can fly at high altitudes (Maina 1989; Scheid & Piiper 1987; Schmidt-Nielsen 1975, 1990).

Rigid lung

The fact that the lungs are rigid and play no role in ventilation means that there is 20% more area for gas exchange than in mammals. However, this rapid efficiency of gas exchange can have its downside as it makes bird much more susceptible to inhaled toxins and infections.

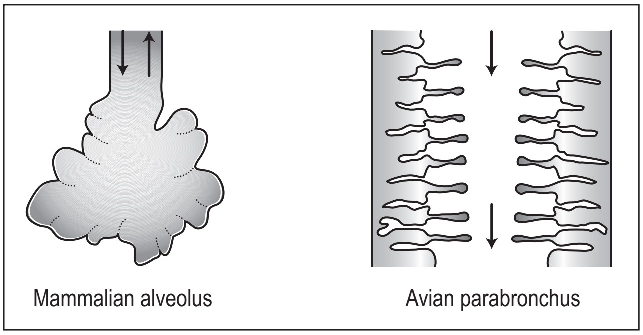


Figure 6.46 • Comparison between mammalian “to and fro” ventilatory system via alveoli and the “flow through” avian system of parabronchi.

Airsacs

These are thin (two cells thick), distensible and transparent sacs, lined by simple squamous epithelium. They constitute 80% of the respiratory volume and extend from the body cavity into the wing, vertebrae, and leg bones (Lasiewski 1972; Maina 1996). There is little blood supply as they play no role in gas exchange (Dyce et al. 2002; Fedde 1993). In most birds there are three pairs of airsacs and two single ones, creating eight in total (Figs. 6.41 and 6.42). In some species the cervical sacs are paired, making nine airsacs (Scheid & Piiper 1987). Each airsac is connected to the secondary bronchi at an area called an *ostium* which is usually located along the ventrolateral border of the lung. The parabronchi also interconnect with all the airsacs except the cervical one.

The airsacs are usually divided into two groups according to their connections to the bronchi: the cranial airsacs (cervical, clavicular, and cranial thoracic), which connect to the ventral bronchi, and the caudal airsacs (caudal thoracic and abdominal), which connect to the primary bronchus (Fig. 6.44).

Function of airsacs

The airsacs function to create a unidirectional flow of air through the lungs, which is important for maximizing oxygen extraction. They help to reduce the amount of heat produced during flight by evaporation from the airsacs. They also play a role in sound production, courtship displays in some species, and possibly cooling of the testes for spermatogenesis.

Cervical airsac

This lies between the lungs, dorsal to the esophagus and has vertebral diverticula from C3 – T5. It can be paired in some birds. It also communicates with the skull via the infraorbital sinus. It may help to provide buoyancy and insulation and reduce the point of impact in diving birds.

Clavicular airsac

This lies in the thoracic inlet and has two parts: the intrathoracic diverticulum around the heart and sternum, and the extrathoracic, which spreads between the bones of the pectoral girdle and into the proximal humerus. This sac extends into the syrinx and is essential for sound production.

CLINICAL NOTE

Compound fractures of the humerus can introduce infection via the pneumatic bones into the lungs and airsacs.

Cranial and caudal thoracic airsacs

Both these sacs are paired and lie in sequence in the dorsolateral thoracic cage. The caudal thoracic airsacs are the only ones which lack a connection with pneumatic bones.

Abdominal airsac

This is paired and reaches from the lungs to the cloaca. It has diverticula around the kidneys and femora. It is potentially the largest in all birds. In the live bird this sac can be entered during laparoscopy, close to the ostium at the angle between the lateral border of the ilium and the caudal border of the dorsal end of the last vertebral rib.

HOW DO BIRDS BREATHE?

Birds do not have a diaphragm so the air sacs act like a bellows to move air through the non-expansile lungs. This is controlled by the action of the muscles, which act independently during flight.

Respiration

Respiration rate

The smaller the bird the faster the respiration rate. It can vary from 40–50 breaths per minute in cockatiels to 25–30 in pigeons and 13 in turkeys. The ostrich with 3–5 breaths per minute has the slowest rate of all (Brackenbury 1987). Flying birds increase their respiration rate by 10–12 times above their resting rate, rising to 20–30 times with maximum exertion.

Muscles of respiration

Respiration is controlled by the external and internal intercostal and abdominal muscles. Birds have the same abdominal muscles as in mammals although, as the sternum is so large, they are smaller. Unlike mammalian ventilation, which takes one respiratory cycle, it takes two ventilation cycles to move air right through the avian system. This does not mean the two cycles are different but that it would take a single bolus of air two breaths before it can be exhaled (McLelland & Molony 1983).

Both inspiration and expiration require active muscle contractions and airflow in the paleopulmonic parabronchi is always in a caudal to cranial direction.

CLINICAL NOTE

The good news is that, because the trachea has rigid rings and the carotid arteries are protected by the cervical vertebrae, it would be difficult to strangle a bird. The bad news is that birds can easily asphyxiate by excessive pressure on their sternum and abdominal muscles, so be careful when handling them (King & Payne 1964).

Inspiration

There are six muscles of inspiration but the principal ones are the external intercostals and the costosternalis. On inspiration the rib cage moves outwards and the sternum moves downward. This negative pressure causes air to be sucked in via the nares to the air sacs. Half of this will enter the caudal airsac via the neopulmonic bronchi and half will enter the cranial airsacs via the paleopulmonic bronchi. No air passes directly into the cranial airsacs (McLelland & Molony 1983).

Expiration

There are nine muscles of expiration, the main ones being the internal intercostal and the abdominal musculature. On expiration the rib cage moves upwards, reducing chest size and compressing air from the airsacs back through the lungs. Air from the caudal airsacs passes through the paleopulmonic bronchi into the cranial airsacs. Air from the cranial airsacs flows out of the primary bronchi and trachea (McLelland & Molony 1983).

CLINICAL NOTE

The avian flow-through system means that artificial ventilation can be achieved by fresh oxygen down the trachea or via an airsac cannula if the trachea is obstructed. Manual compression by compressing and lifting the sternum can also be undertaken (Powell 2000).

KEY POINTS

- Birds have no diaphragm.
- The trachea is longer and much wider than in mammals, creating more dead space.
- The location of the syrinx at the bifurcation of the trachea means this is commonly a site for foreign body blockage.
- Birds have increased their oxygen absorption by separating gaseous exchange from ventilation, having a thin blood–air barrier, cross-current exchange, and a flow-through system.
- Airsacs function solely in ventilation; as they are poorly vascularized the caudal airsacs easily harbor infections.
- Airsac cannulation can be life saving in cases of obstructive dyspnea.

DIGESTIVE SYSTEM

The avian gastrointestinal tract (Figs. 6.52 and 6.53) is relatively short, with low volume to keep the bird lightweight for flight. Consequently, birds ingest small amounts frequently and extract energy and nutrients rapidly to sustain their high metabolic rate. Transit times ranging from as little as 16 minutes to 2 hours are found in passerines. Birds also have

CLINICAL NOTE

Macrophages in the parabronchial epithelium filter out a lot of potential pathogens. The cranial airsacs are consequently filtered more than the caudal airsacs and this means a disease like aspergillosis is much more common in the caudal airsacs (Fedde 1993) (Fig. 6.47).

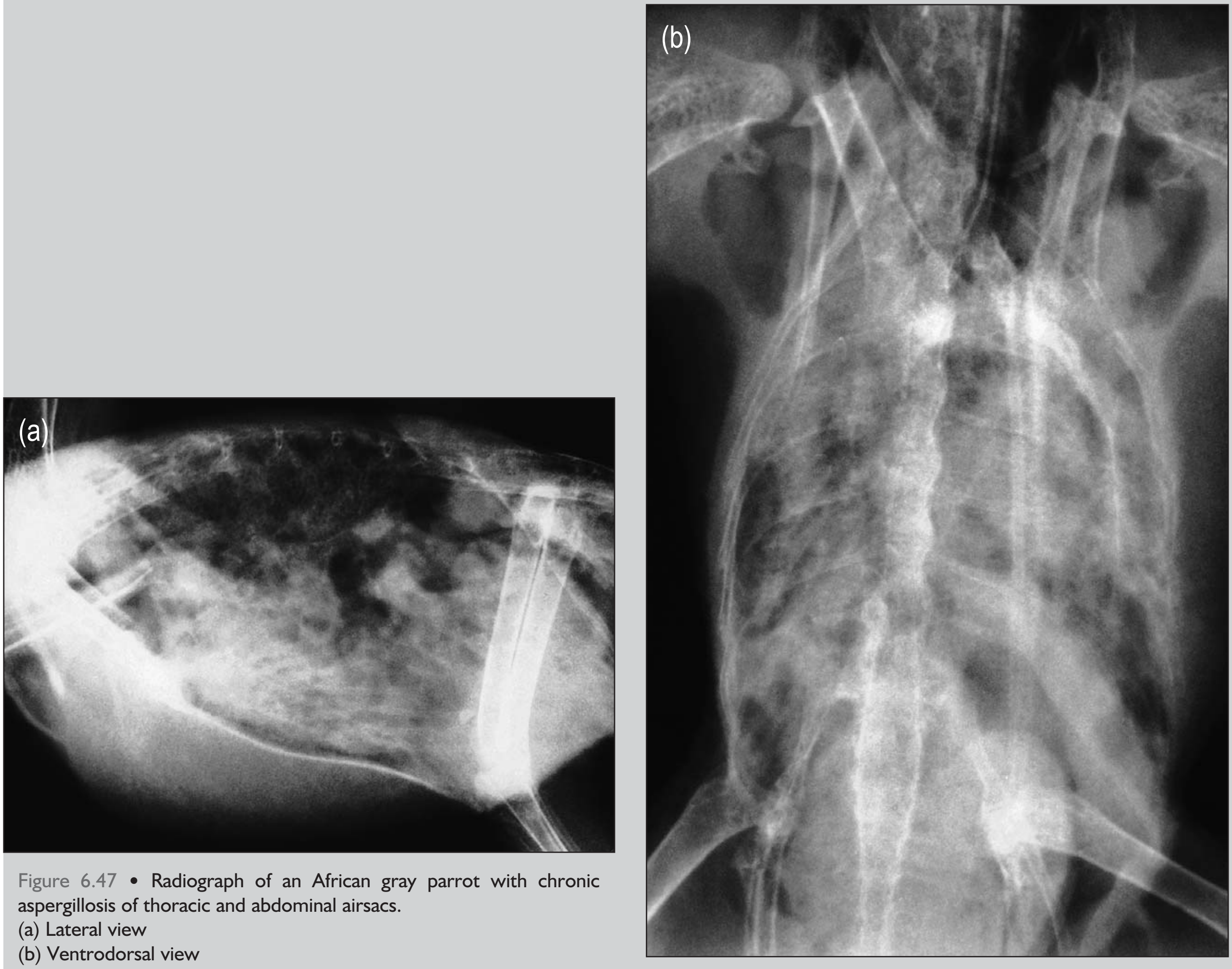


Figure 6.47 • Radiograph of an African gray parrot with chronic aspergillosis of thoracic and abdominal airsacs.
(a) Lateral view
(b) Ventrodorsal view

an extremely efficient digestive system, passing remarkably small amounts of excreta in contrast to the amount of food eaten.

Birds have no teeth so no time is spent on chewing and food passes rapidly to the crop for storage and into the gizzard for mechanical digestion. This heavy organ located at the bird's center of gravity has taken on the role of mammalian molars in grinding down the unmasticated food. Herbivorous birds like the ostrich and chicken also have well-developed ceca for food breakdown.

Beak

The beak (synonym bill) replaces the lips and teeth of mammals and consists of bone, vascular dermis and a modified heavily keratinized, germinal layer. The keratin layer of the beak is called the *rhamphotheca*, with the *rhinotheca* covering the upper beak and the *gnathotheca* covering the lower beak. The lower beak slips inside the upper beak, fitting into a notch on the roof when the jaws are closed. Soft folds of keratin at the angles of the mouth form the rictus.

CLINICAL NOTE

Birds have low fat reserves due to the negative effects of excess weight. Small birds like budgies and canaries should not be fasted prior to anesthesia as they have low glycogen reserves and rapidly become hypoglycemic.

The epithelium has a very thick stratum corneum that contains hydroxyapatite, calcium, phosphate, and keratin and gives the beak its hardness. The vascular dermis is extremely thin and is sandwiched between the horny epidermis above and the periosteum of the premaxilla and mandible below.

Beak keratin appears in two forms. The weight bearing horn (*tomia*) found at the cutting edges and tips of both beaks performs the function of teeth in cutting up food. A second covering horn lies externally on the non-contact surface of the beak. Newly hatched chicks have a horny pro-

BEAK & TONGUE MODIFICATIONS IN WATERFOWL

Many waterfowl have modified their beak and tongue into a specialized filter system for sifting out food particles from water. Ducks, geese, and swans have a thick, fleshy tongue with the rostral border modified into a scoop with bristles on the lateral margins. There is a shallow median groove on the dorsal tongue and a flesh caudal eminence, the torus linguea. The upper and lower beak have lamellae into which the bristles fit (Fig. 6.48). Water is sucked in to fill the dorsal groove in the tongue and this is then pressed against the palate and filtered laterally by the bristles, which retain the food particles. In some species the bill tip contains sensory organs called Herbst corpuscles in the dermis to help discriminate food particles while feeding (McLelland 1979).

Flamingos have a specialized beak that filters organisms from the mud or water. At hatching the bill is straight but develops a bend when the beak matures. The bird feeds with the bill inverted so that the mandible is uppermost. The piston-like tongue moves food and water in and the solid particles are filtered out by the lamellae of the upper and lower beak (Fig. 6.49).

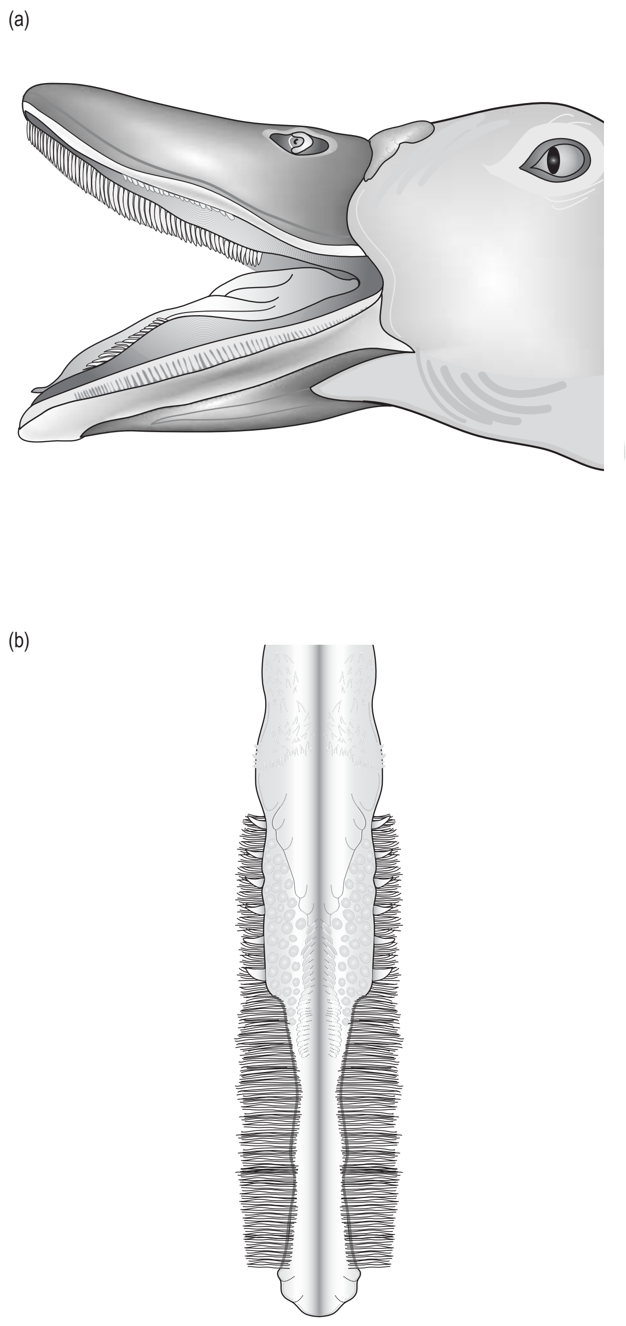


Figure 6.48 •
(a) Beak of duck showing upper and lower lamellae
(b) Tongue of duck showing lateral bristles – these bristles press against the lamellae to filter out the food particles

jection on the rostral beak called the egg tooth, which is used to pip the shell.

Cere

The base of the dorsal maxillary rhamphotheca is called the *cere* and it can be naked or fully feathered. It is composed of softer keratin than the rest and is particularly prominent and fleshy in waterfowl.

CLINICAL NOTE

The male budgie has a blue cere while the hen has a brownish pink cere. Male budgies however can develop a brownish cere under the feminizing influences of testicular Sertoli cell tumors.

Function of the beak

One of the main functions of the beak is to apprehend food and prepare it for delivery into the esophagus. However, the beak also has many other roles like preening, courtship, nest making, and the feeding of chicks. In psittacines the beak is also used for locomotion and in these species the beak is connected to the skull by a synovial hingelike joint.

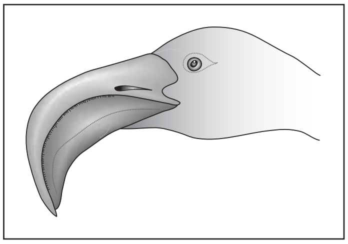
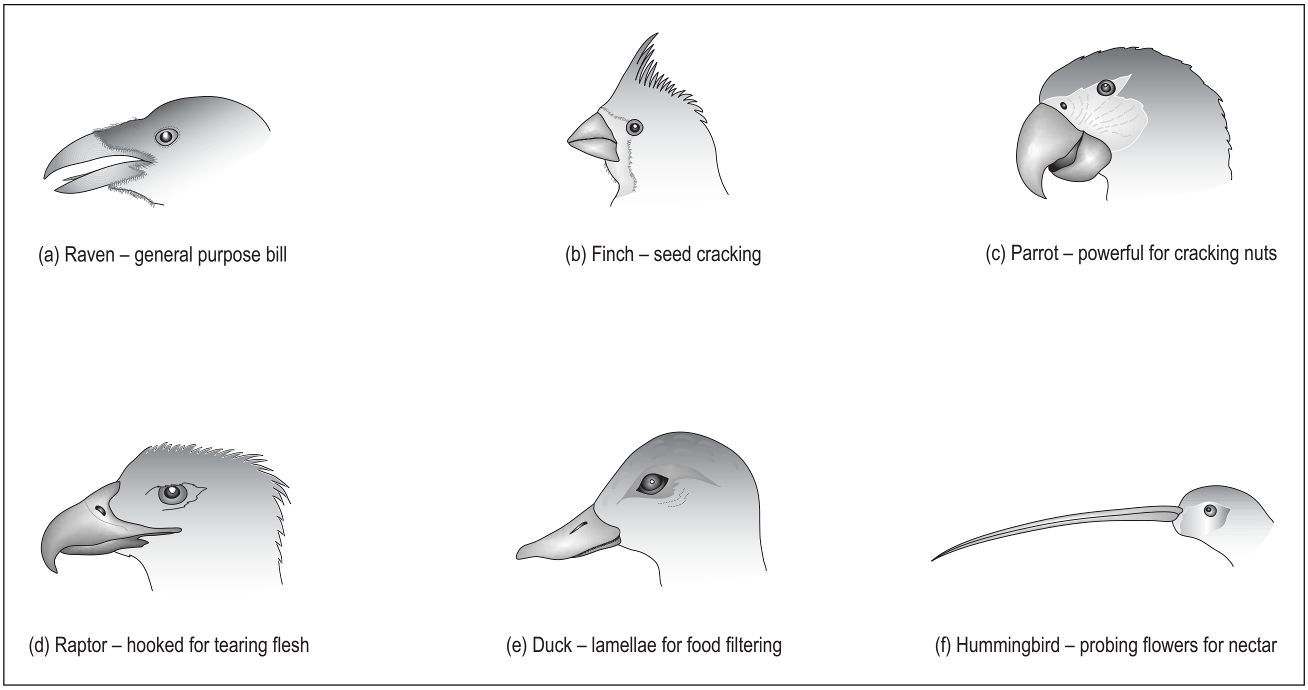


Figure 6.49 • The flamingo has a specialized bill that enables it to filter out its food from the water.

Beaks are widely modified according to diet (Fig. 6.50). For example, finches have a stout conical bill for cracking seeds. In some species ridges on the hard palate serve to wedge the seed in place in order to crack open the shell with the lower beak. Hummingbirds have a long probing bill to penetrate deep into flowers for nectar. Raptors have hooked beaks for tearing prey while crows have a strong and pointed beak suited for their omnivorous diet.

CLINICAL NOTE

The powerful beak of psittacines is strong enough to crack a Brazil nut, so mind your fingers when examining large parrots.



(a) Raven – general purpose bill

(b) Finch – seed cracking

(c) Parrot – powerful for cracking nuts

(d) Raptor – hooked for tearing flesh

(e) Duck – lamellae for food filtering

(f) Hummingbird – probing flowers for nectar

Figure 6.50 • Modifications of beak according to diet.
(a) Raven – general purpose bill
(b) Finch – seed cracking
(c) Parrot – powerful for cracking nuts
(d) Raptor – hooked for tearing flesh
(e) Duck – lamellae for food filtering
(f) Hummingbird – probing flowers for nectar

Oropharynx

In mammals the glossopalatine arches divide the oral cavity from the pharynx, and the soft palate divides the nasal cavity and oral pharynx. Birds, however, only have a common cavity called the *oropharynx*, which is often highly colored in newly hatched passerines to attract the parents attention while gaping for food (Klasing 1998). The hard palate is incomplete with a median slit called the choana, which links the nasal cavity to the oropharynx. This closes when food is swallowed to stop food entering the nasal cavity (Fig. 6.51). The oropharynx is lined by stratified squamous epithelium which is keratinized into papillae that line the oropharynx along the roof, choanal margins, infundibular cleft, and tongue to the laryngeal mound. These play a role in helping the food to pass caudally (King & McLelland 1984).

The infundibular cleft is a midline slitlike opening lying caudal to the choana, which is the common opening for the pharyngotympanic tubes (the avian equivalent of eustachian tubes). In birds these are short and not covered by folds in order to stop excess pressure building up in the middle ear when the bird flies (Hoefer et al. 1997; King & McLelland 1984). Lymphatic tissue called the pharyngeal tonsils lie in this cleft as well. The choana and infundibular cleft have a common opening in some birds like budgies (*Melopsittacus undulatus*) (Dyce et al. 2002).

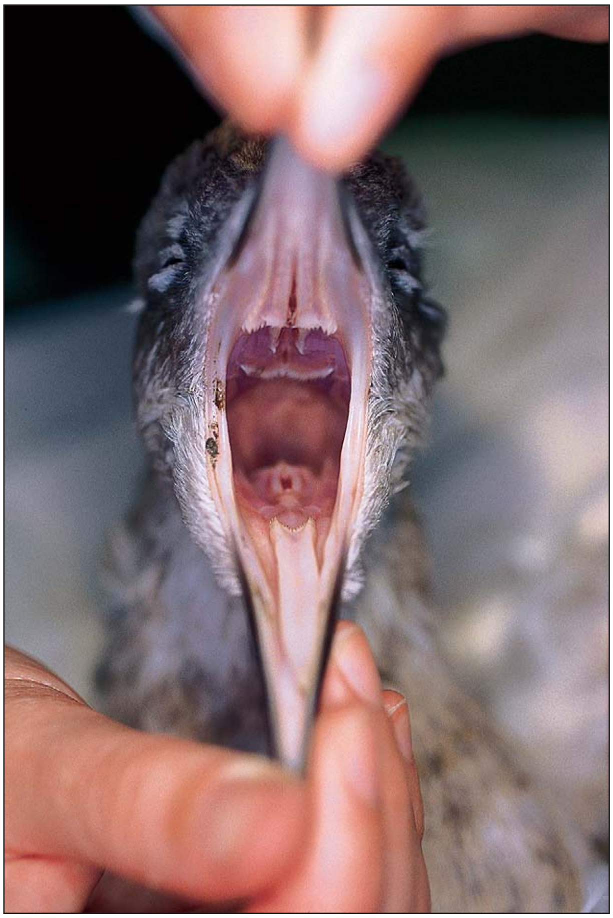


Figure 6.51 • Open mouth view showing choana, glottis and triangular tongue.

CLINICAL NOTE

Many psittacines with Vitamin A deficiency develop blunted choanal papillae due to squamous metaplasia. These block salivary ducts and cause secondary bacterial infection; hence abscesses are commonly seen under the tongue and around the choana.

CLINICAL NOTE

When performing crop lavage under anesthetic it is important to block off the choana as well as inserting an endotracheal tube to avoid food entering the nasal cavity.

Tongue

The avian tongue is a highly diverse organ and can be used for both collecting, manipulating, and swallowing food, depending on the species (Table 6.4). In most species it is non-protrusible. It is supported by the hyobranchial (hyoid) apparatus, which consists of a rostral rod, the entoglossal bone, and a caudal rod, the rostral basibranchial bone. In most species the tongue itself is merely cornified mucous membrane covering the hyoid bone. Psittacines are unique in having paired entoglossal bones and a large muscular tongue capable of amazing dexterity (King & McLelland 1984).

Birds appear to have a poorly developed sense of taste, perhaps because of the rapid transit of food from mouth to crop. Taste buds are few in number and located on the palate, the base of the tongue, and the floor of oropharynx (see Senses).

Salivary glands

Birds have practically a layer of salivary glands scattered throughout the oropharynx. These are not well defined but there are small aggregates of maxillary and palatine glands in the roof of the mouth, and mandibular and lingual glands on the floor. Avian saliva is very different to the water secre-

Table 6.4 Tongue types and functions (King & McLelland 1984)

Role of tongue	Type of species	Tongue type
Collecting food	Woodpeckers, hummingbirds	Protrusible
Manipulating food	Parrots, raptors, ducks, geese, swans	Short, non-protrusible, caudal papillae
Swallowing food	Crows, domestic fowl	Non-domestic fowl protrusible, caudal papillae

GENERAL INTEREST

In some birds like woodpeckers the hyoid horns are so elongated they go completely around the back of the skull, ending near the upper maxilla. This enables the woodpecker to protrude their tongue over four times the length of the upper beak to catch insects. Woodpeckers also have large mandibular glands beneath the tongue that secrete a sticky fluid to coat the tongue and act like flypaper to trap insects.

tions of mammals as it is more mucoid to help lubricate food. Production of saliva is under the control of parasympathetic stimulation and is especially well developed in birds that eat a lot of dry food, such as insects or seeds (Duke 1986, 1993; Hoefer et al. 1997).

GENERAL INTEREST

Swifts secrete a mucilaginous substance from their mandibular glands, which is used like cement for their nests. In the *Collocalia* swift species of SE Asia the nest is built entirely of saliva and forms the gourmet Asian dish of bird's nest soup (King & McLelland 1984; McLelland 1979).

Feeding

The beak prehends the food, which is then lubricated by sticky mucus produced from the salivary glands. The lack of soft palate and pharyngeal muscles means that birds do not use peristalsis for swallowing. Instead papillae on the tongue and palate and rostrocaudal movement of the tongue moves the food into the caudal oropharynx. The head is then raised to let the food move passively, the glottis and choana close over and food gets flushed by the saliva into the proximal esophagus. From there it moves by peristaltic action down the gastrointestinal tract (Duke 1986, 1993; Hill 1971b; McLelland 1979).

Drinking

The beak is immersed in water and fluid enters the mouth by rostrocaudal movement of the tongue. Once in the caudal oropharynx the head is raised and it passes into the esophagus by gravity. Pigeons manage to suck water and do not have to raise their head while drinking; hummingbirds suck nectar through a tubular tongue. Psittacines can lap water due to their muscular tongue (King & McLelland 1984; McLelland 1979).

Esophagus

The esophagus lies to the right side of the neck, is thin walled and has longitudinal folds, which enables it to be more distensible than in mammals. It is lined by stratified squamous epithelium with mucous glands to aid the passage of food down the tract. It contains only smooth muscles innervated by the vagus nerve, so excitement or fear can influence motility. Paralysis of the esophagus can occur in heavy metal poisoning causing stasis and impaction.

Regurgitation

This is when food is brought back by antiperistaltic movement of the esophagus. It is normal in species like pigeons and penguins while they are nursing neonates and is also used for sexual display in species like budgies.

Crop (Ingluvies)

This is a dilation of the esophagus located at the base of the neck just cranial to the thoracic inlet. It has the same epithelial structure as the esophagus but no mucus glands (Hill 1971a; King & McLelland 1984). In psittacines it is placed transversely and is easy to palpate as it is strongly attached to skin. The crop of pigeons is well developed and bilobed whereas waterfowl have a barely visible fusiform widening of the esophagus (Fig. 6.55).

CLINICAL NOTE

Crop impaction can be caused by ingesting large amounts of dry food. In raptors it can be blocked by the fur and feathers of prey if there is inadequate moisture in the diet (King & McLelland 1984).

The function of the crop in birds like psittacines and pigeons is to store food when the stomach is full (Evans 1996). In some birds, such as domestic fowl, harder food like grain is softened in the crop before traveling on to the proventriculus for physical digestion. In species like owls, gulls, and penguins, which have no crop, food is either stored in the esophagus or passes directly into the proventriculus. Food like fish can often be seen stretching from the proventriculus and sticking out of the beak in piscivorous birds without causing any choking or discomfort (Klasing 1998).

There is little chemical digestion in the esophagus and crop although salivary amylase may initiate carbohydrate digestion. The crop pH is acidic (4–6). It contains some gram-positive bacteria and a small amount of *Candida* species.

GENERAL INTEREST

The Hoatzin bird uses its extensive crop as a gizzard to help physically digest the leaves it feeds on. In these species the mass of the crop is 50 times that of the gizzard (Evans 1996; McLelland 1979).

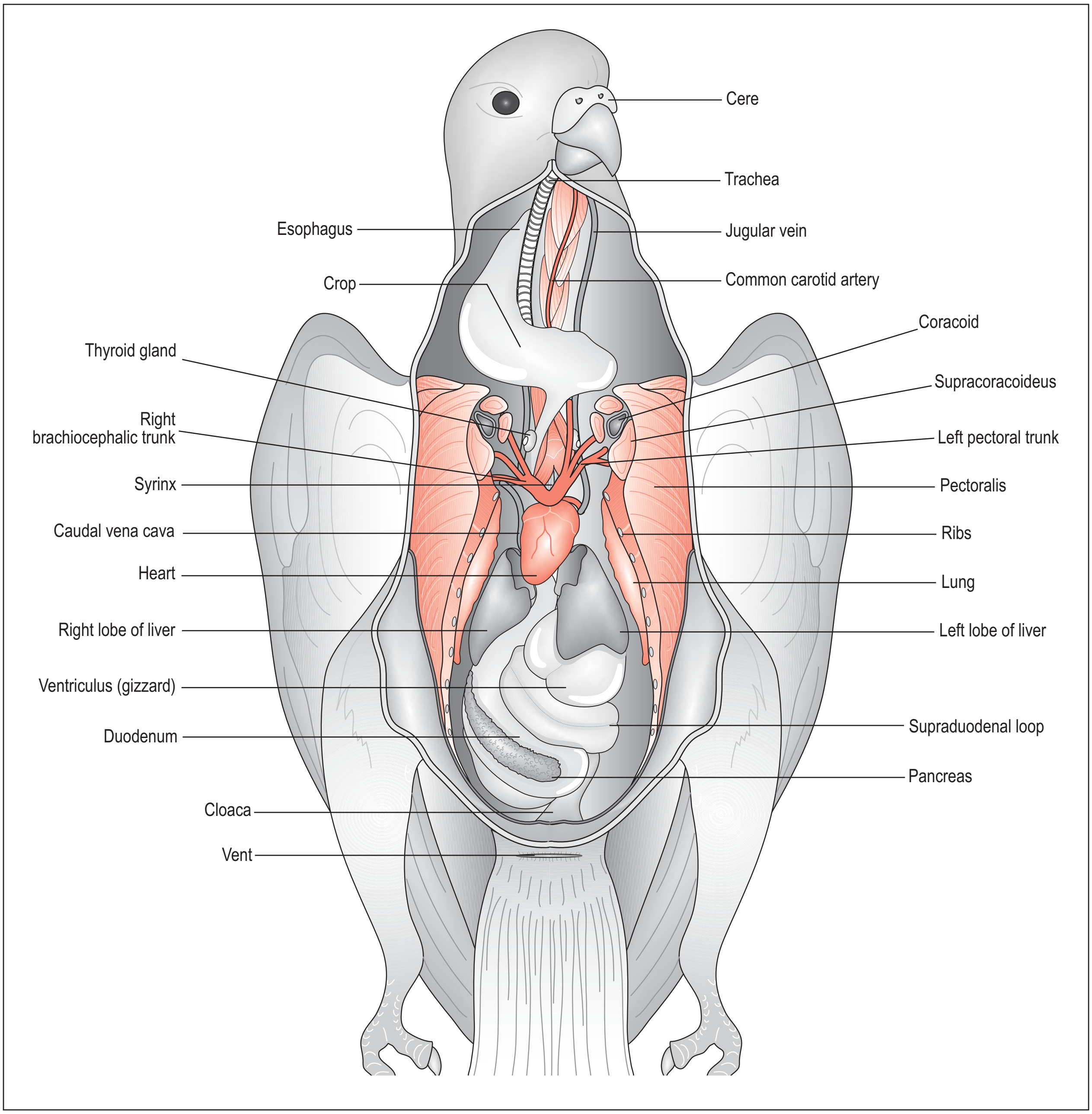

Cere
Trachea
Esophagus
Jugular vein
Crop
Common carotid artery
Coracoid
Thyroid gland
Supracoracoideus
Right brachiocephalic trunk
Left pectoral trunk
Syrinx
Pectoralis
Caudal vena cava
Ribs
Heart
Lung
Right lobe of liver
Left lobe of liver
Ventriculus (gizzard)
Supraduodenal loop
Duodenum
Pancreas
Cloaca
Vent

Figure 6.52 • Ventral view of psittacine showing viscera (sternum and abdominal muscles removed). The lungs lie dorsally so are not very visible.

Crop milk

Columbiformes produce crop milk to feed their young in the first few days after hatching. This is stimulated by prolactin and resembles milk, except it has no carbohydrate or calcium. It is produced in both sexes by desquamating cells from the stratified squamous epithelium of the crop and lasts until about 2 weeks after hatching. Psittacines, finches and Emperor penguins also produce crop secretions (McLelland 1979).

CLINICAL NOTE

The avian esophagus is very distensible so large tubes can be passed when gavage feeding to prevent the risk of accidental intubation of the trachea. For crop sampling, pass a tube into the crop and infuse some warm physiological saline. Aspirate a sample back and perform a wet smear and diagnostic cytology.

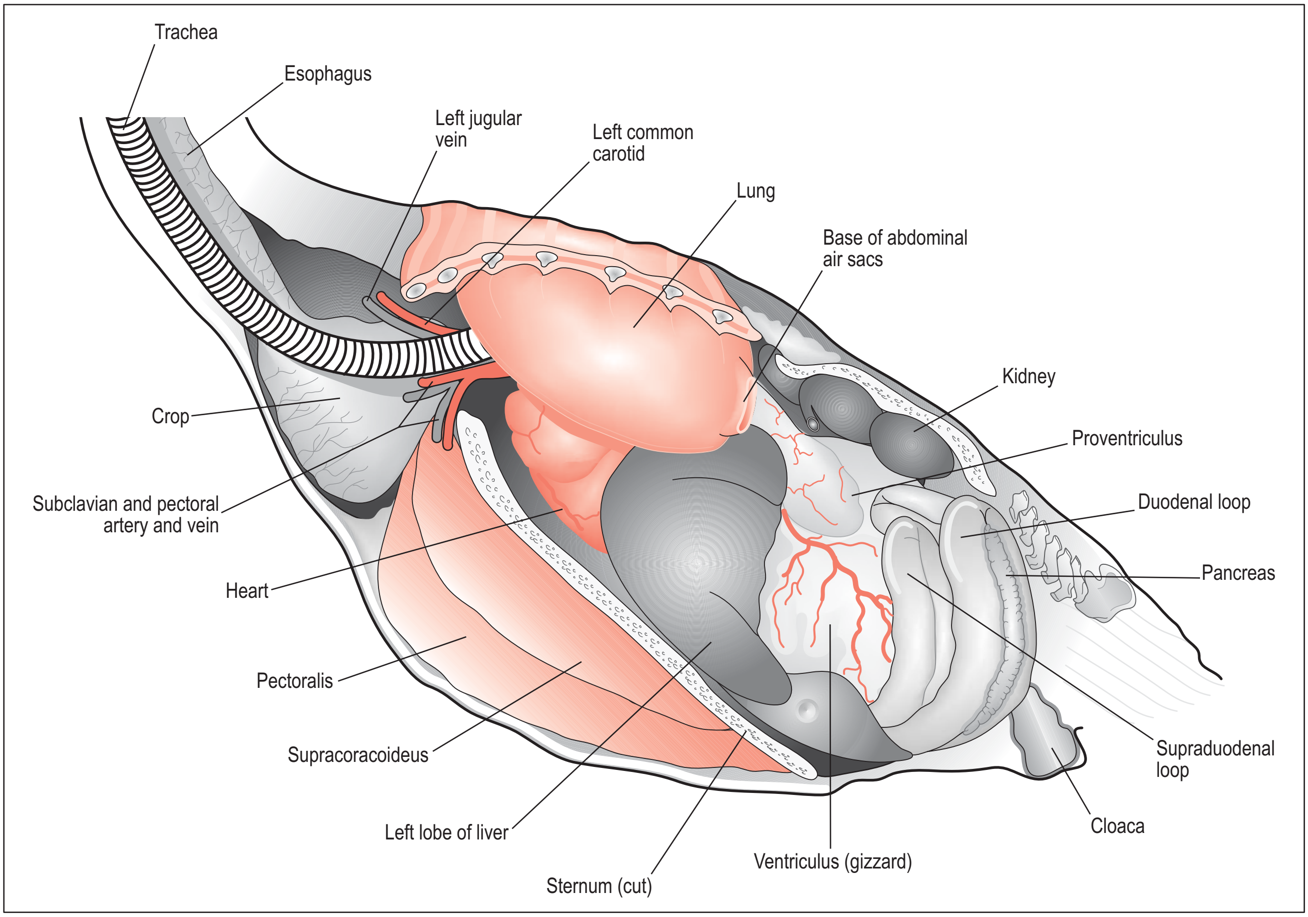

Trachea
Esophagus
Left jugular vein
Left common carotid
Lung
Base of abdominal air sacs
Kidney
Proventriculus
Duodenal loop
Pancreas
Crop
Subclavian and pectoral artery and vein
Heart
Pectoralis
Supracoracoideus
Left lobe of liver
Sternum (cut)
Ventriculus (gizzard)
Supraduodenal loop
Cloaca

Figure 6.53 • Lateral view of psittacine showing lungs and viscera.

Stomach

In birds the stomach is divided into the glandular proventriculus and the muscular ventriculus (gizzard) divided by an isthmus. There are two types of stomach according to the diet of the species (Denbow 2000).

Carnivorous birds

These fish and meat eating species have little difference between the two stomachs, having a large easily distensible stomach to contain whole prey. The ventriculus in these species is used mainly for allowing time for gastric juices to act on the soft food rather than physical digestion (McLelland 1979).

Granivorous birds

These birds eat relatively indigestible foods so need a gizzard for grinding food. Consequently they have a thick-walled, non-distensible, and glandular proventriculus and a thick, muscular ventriculus (Figs. 6.56 and 6.57). Proventriculectomy is not easy in these species.

Proventriculus

This is the glandular portion of the stomach and its main function is production of the gastric juices and propulsion of food into the gizzard. It has two cell populations: epithelial cells that produce mucus and oxynticopeptic cells, which produce pepsinogen and hydrochloric acid (Denbow 2000; Hill 1971a). It lies to the left of the midline in the cran-

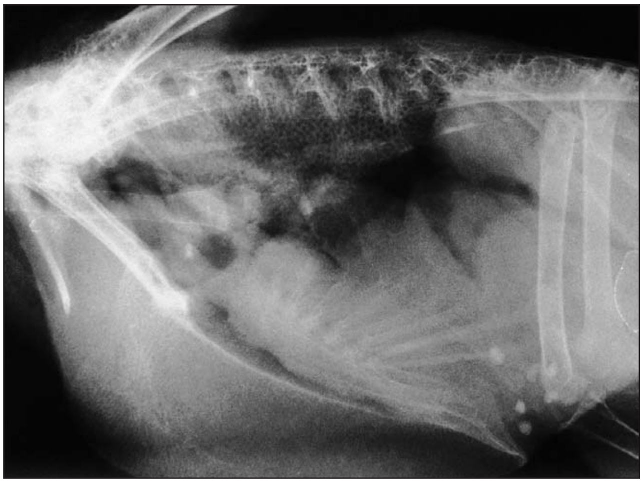


Figure 6.54 • Lateral radiograph showing normal honeycomb lungs, gizzard located at level of acetabuli and large pectoral muscle mass. This bird had renomegaly secondary to lymphoma.

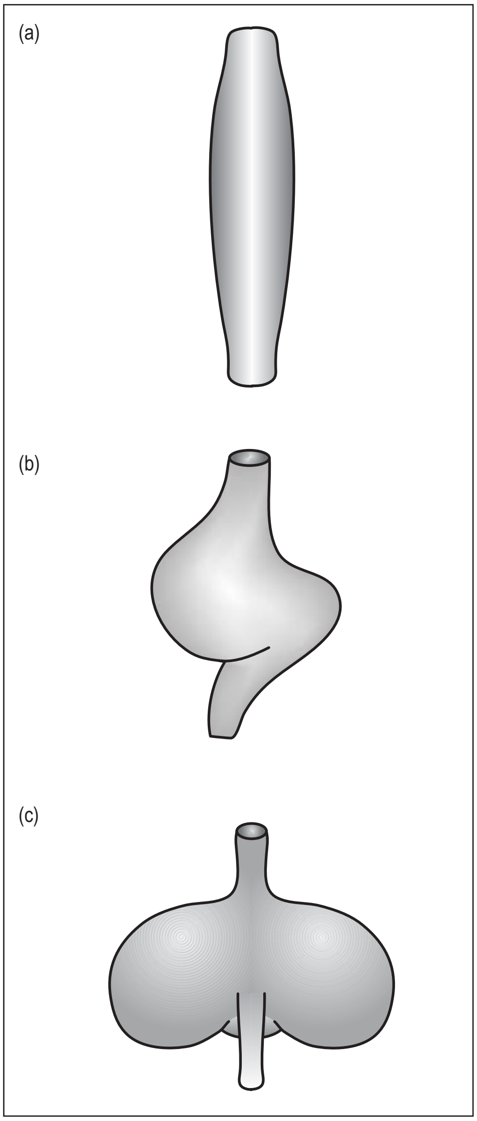


Figure 6.55 • The shape of the crop depends on the bird's diet.
(a) Waterfowl – simple and fusiform
(b) Parrots – seed can be softened here prior to passing into the ventriculus
(c) Pigeons – well developed and bilobed for softening grain and production of crop milk

iodorsal celom and is covered by other abdominal organs and the post-hepatic septum. There is no distinct esophageal sphincter and the loss of longitudinal folds is the only differing feature between esophagus and stomach.

Isthmus (Intermediate zone)

This is the transition from glandular stomach to muscular gizzard. It has no glands so the wall is thinner and less rigid than the proventriculus.

Ventriculus (Gizzard)

The ventriculus lies to the left of the midline and can be palpated as a firm mass just caudal to the sternum (Fig. 6.54). This second stomach is the site of protein digestion and mechanical breakdown of food and consists of a large volume of smooth muscle lined internally by columnar epithelium. Koilin lines this epithelium like a cuticle and helps protect it during the grinding process. It is formed from mucosal cell secretions and is composed of protein and carbohydrate and becomes stained yellow-green due to bile reflux from the duodenum (Denbow 2000).

Herbivores (granivores) like turkeys and waterfowl tend to have a very developed ventriculus but it is less muscular in psittacine species that dehusk their seeds prior to swallowing (Klasing 1998; McLelland 1979).

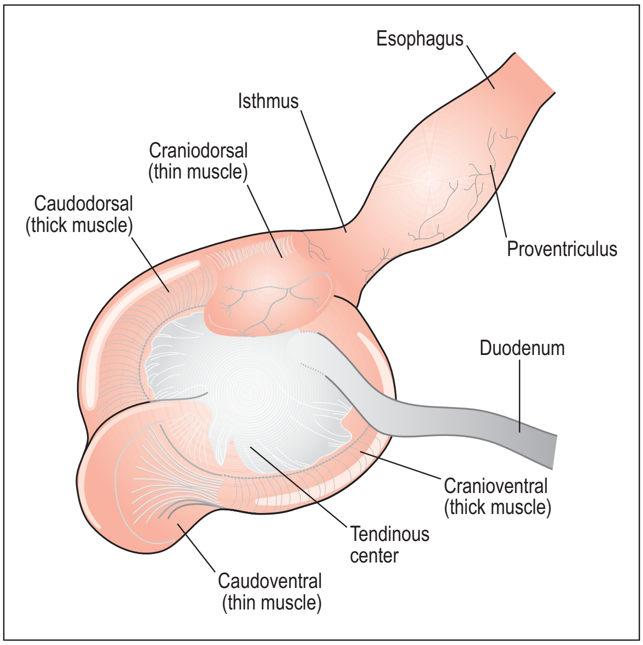

Esophagus
Isthmus
Craniodorsal (thin muscle)
Caudodorsal (thick muscle)
Proventriculus
Duodenum
Cranioventral (thick muscle)
Tendinous center
Caudoventral (thin muscle)

Figure 6.56 • External appearance of ventriculus (gizzard) in granivorous bird showing well-developed grinding muscles.

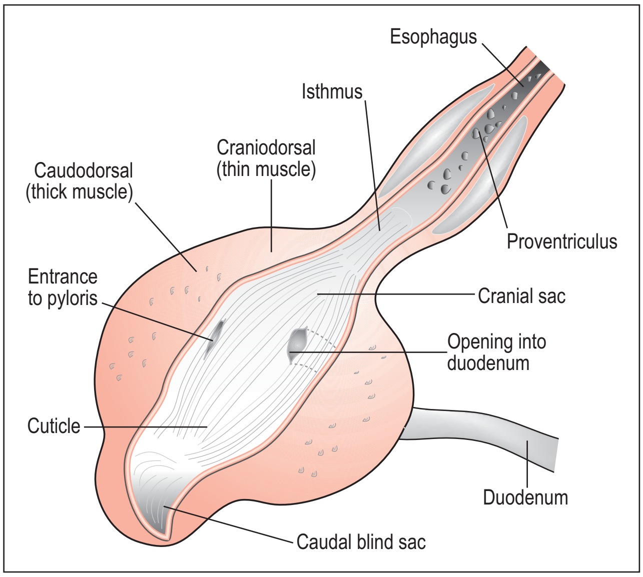

Esophagus
Isthmus
Craniodorsal (thin muscle)
Caudodorsal (thick muscle)
Proventriculus
Entrance to pyloris
Cranial sac
Opening into duodenum
Cuticle
Duodenum
Caudal blind sac

Figure 6.57 • Cross-section of ventriculus of granivorous bird.

CLINICAL NOTE

The ventriculus can be the site of foreign bodies so, if one has to be removed, the blind thin muscular sacs cranially and caudally are the best site for ventriculectomy incisions. Waterfowl can also pick up lead weight which can be ground down by the contractions causing the lead to be absorbed.

The ventriculus has four muscular bands arranged so as to provide rotary and crushing movements to aid mechanical digestion. These consist of two thick layers of circular, smooth muscles that attach to a central tendinous aponeurosis on the left and right. They are dark colored due to the high myoglobin content of the smooth muscle. Cranially and caudally there are blind sacs formed by two layers of paler, thin muscles (King & McLelland 1984).

GENERAL INTEREST

The pulverizing action of the gizzard muscles is immensely powerful. In some bizarre medieval experiments performed on turkeys it was found that the gizzard could crush 24 walnuts in their shells in under 4 hours and turn 16 surgical lancets into grit in 16 hours!

CLINICAL NOTE

Psittacine and passerine species do not require grit for digestion as they crack open seeds and eat only the kernels. Chickens and pigeons swallow their seed whole and grind them in their gizzard using grit. Although grit is not essential in these species it markedly reduces gut transit times. Coarser food will require coarse grit (Duke 1986, 1993; Hoefer et al. 1997; McLelland 1979).

Food moves back and forth between proventriculus and ventriculus by contraction of the thick and thin muscles during stomach digestion. The opening of the duodenum lies very close to the proventriculus so that food not requiring grinding can bypass the gizzard completely.

Intestinal reflux

Intestinal reflux (also called egestion or casting) is performed by carnivores like Strigiformes (owls) and Falconiformes and is the method used to void indigestible portions from the ventriculus. It occurs due to synchronized contractions of the proventriculus, ventriculus, and duodenum about 12 hours post feeding. The presence of bulky food items in the stomach causes gastric contractions to increase and compact the pellet and push it into the distal esophagus. During reflux, gastric motility is inhibited and the pellet is expelled through the mouth by esophageal antiperistalsis.

The content and timing of the pellet depends on the bird's feeding habits. Owls eat their prey whole and have no crop for storage, so they egest bone as well as the usual roughage of feathers and fur after every meal. Falconiformes tear their food apart with their talons and, having crops, hold the food for longer and digest all the bone portion. They egest just once daily or at dawn as part of the circadian rhythm (McLelland 1979).

Pylorus

This lies to the right of the ventriculus. It is small in chickens but very large and dilated in cormorants and herons, perhaps to delay indigestible debris like fish bones for longer before entering the duodenum.

Liver

The liver is yellow color in a newborn chick because of the high fat content resulting from the absorption of yolk (McLelland 1979). This changes to the usual red-brown at around 10 days of age. It is proportionately large for the bird's size, compared to mammals. There are two main liver lobes, which surround the heart and join cranially at the midline. Some lobes are frequently subdivided. The liver is covered by a fat-filled post-hepatic septum. There is a well-developed hepatic portal circulation and the caudal vena cava enters the dorsal portion of the right lobe. The gall bladder lies on the visceral surface of the right lobe (King & McLelland 1984).

The gall bladder is absent in some Psittaciformes, Columbiformes, and Struthioniformes (Bezuidenhout 1999; Evans 1996). In these species the bile flows from the right liver lobe to the ascending duodenum via the hepatoenteric duct.

Bile is important for avian digestion as it aids the emulsification of fats and also contains amylase and lipase. Many birds lack the enzyme bilirubin reductase so biliverdin is the main bile pigment (McLelland 1979). The liver synthesizes bile acids and empties them directly into the duodenum where they are reabsorbed and sent back to liver by enterohepatic circulation. Therefore, hepatic malfunction can be measured by raised bile acids.

CLINICAL NOTE

A bird with liver problems will often pass urates stained green by the bile pigment biliverdin. Raised bile acid can also be a good indicator of hepatic disease.

CLINICAL NOTE

Some birds like Mynah birds and toucans store high levels of iron in their hepatocytes, leading to hemochromatosis or iron storage disease. The cause is unknown but it can be treated by recurrent phlebotomies to remove excess iron and by feeding a diet low in citrus fruits.

Pancreas

This is pale pink and lies within the antimesenteric border of the duodenal loop. It is composed of three lobes with one to three ducts that secrete the pancreatic enzymes into the ascending duodenum near the bile ducts. As in mammals, this gland has both endocrine and exocrine functions. It secretes the enzymes amylase, lipase, trypsin, and chymotrypsin and these help the breakdown of carbohydrates, fats, proteins, and bicarbonate. These are produced under the control of the hormone secretin and the vagus nerve (King & McLelland 1984).

Small intestine

In general, the small intestine is relatively shorter than in mammals but it is highly convoluted to help with birds' high metabolic demands. It is separated from the body wall by the caudal thoracic and abdominal airsacs. There is very little histological difference between the duodenum, ileum, and jejunum, which form a series of narrow u-shaped loops on the right side of the celom (McLelland 1979). The axial loop carries the Meckel diverticulum and marks the boundary between the ileum and jejunum, while the supraduodenal loop is the most distal part of the ileum (Evans 1996; King & McLelland 1984).

CLINICAL NOTE

The duodenum is easily seen on exploratory and necropsy as it lies most ventrally – caution must be taken to avoid incising it when entering the celomic cavity.

The bile and pancreatic ducts open into the distal part of the ascending duodenum opposite the cranial part of the gizzard. The jejunum and ileum are demarcated by the yolk sac remnant, the Meckel diverticulum. Altricial birds are fed by their parents so absorb the yolk sac speedily after hatching. Precocial birds have to fend for themselves from early on so rely on the yolk sac for nourishment during this period. It is normally absorbed from 10 days post hatching, leaving scar tissue behind.

The intestines are thin walled and narrow and consist of mucosa, submucosa, circular and longitudinal muscle, and serosa. The intestinal epithelium has folds and villi but, unlike in mammals, does not contain lacteals (Hill 1971a; McLelland 1979). Instead they absorb lipids through a well-developed capillary network. Three types of epithelial cell exist: chief cells, goblet cells, and endocrine cells. The chief cells have a brush border to absorb food, the goblet cells secrete mucus, and endocrine cells produce the hormones somatostatin, gastrin, and secretin. Although birds lack true mesenteric lymph nodes they have lymphoid nodules (Peyer patches) in the lamina propria to provide lymph drainage.

Large intestines

There is a short colorectum, which extends from the ileocecal junction to the cloaca. The colon is no thicker than the small intestine and reabsorbs water and electrolytes by antiperistaltic movements (Duke 1993). Urine is moved from the cloaca into the colon by this method.

Ceca

These are paired and arise at the junction of the ileum with the rectum. They run retrograde from the ileocecal junction with their blind end lying near the cloaca.

The mucosa has villi and there are scattered lymph follicles in the wall. The main function of the cecum is to aid the digestion of cellulose so they are most prominent in ground dwelling, flightless birds like ostriches and fowl (Bezuidenhout 1999; Hill 1971b). They are poorly developed in most arboreal birds, being rudimentary in pigeons and passerines and absent in raptors and psittacines (Duke 1993; Evans 1996; King & McLelland 1984). In fact more than two thirds of birds either have no ceca or have rudimentary ones (Klasing 1998).

Role of intestines and cecum

The small intestine is the principal site for chemical digestion. If ceca are present they contain gram-positive bacteria and protozoa which help to digest cellulose in herbivorous species.

Cecotrophy

Some species use cecotrophy to help survival on rough forage. Food passes down the intestines to the coprodeum by peristalsis. Occasionally an unknown mechanism returns the ingesta by retroperistalsis back up to the cecum. The long villi in the cecum separate the nutrient-rich food from the indigestible portion. High nutrient particles are absorbed and the rest is passed distally in a powerful cecal contraction to re enter the cloaca as cecal droppings. These semi-solid, chocolate-brown droppings are normally discharged about once a day (Duke 1986, 1993).

Cloaca

This is the site for termination of the urogenital and digestive systems. It is usually a bell-shaped dilation at the end of the rectum and consists of the copradeum, urodeum, and proctodeum (King, AS 1981a). The Bursa of Fabricius is located in the dorsal wall. The cloaca lies in the midline in mature males but in mature females the enlarged left oviduct pushes it to the right.

Coprodeum

This cranial compartment is where the rectum empties. This largest chamber is an extension of the colon. In some species it is lined by villi and is a site of water absorption. It is separated from the urodeum by the coprourodeal fold. If the rectum is full of feces this fold can bulge out of the vent dispelling feces without mixing them with urates. This fold can also close the coprodeum during egg laying to prevent feces being expelled at the same time (King & McLelland 1984).

Urodeum

This middle compartment is separated from the other parts by the circular mucosal folds. The ureters and genital ducts empty into its dorsal wall. The left oviduct opens into a small mound, which is covered by a small membrane in ducks, geese, and swans until the bird reaches sexual maturity. In male passerines the terminal vas deferens dilates during the breeding season to form a conical projection in the cloaca called the *seminal glottus* or *cloacal promontory* (Lake 1981).

Proctodeum

This is a short compartment separated from the urodeum by the uroproctodeal fold. It empties contents into the vent, which is controlled by the external anal sphincter. The Bursa of Fabricius is located in its dorsal wall. It is the site of B-lymphocyte production and differentiation, which are necessary for humoral immunity. Male ducks, geese, and swans have a large proctodeum to house the large protrusible phallus on the ventral floor.

Vent

This is the external opening of the cloaca. In psittacines this is a circular opening, but it is transverse in domestic fowl and 'u'-shaped in ducks and geese. The sphincter muscle has an outer and inner circle of striated muscle. There is also a transverse muscle that originates from the pelvic bone, passes ventral to the proctodeum, and helps pull the vent into position for copulation.

KEY POINTS

Modifications of the avian gastrointestinal tract:
- Teeth replaced by horny beak
- No soft palate so single large oropharynx
- Open pharyngotympanic (eustachian) tubes
- Esophagus is on the right side of the neck and length and diameter are greater than in mammals
- Lots of mucoid saliva produced to lubricate food
- Crop stores and softens food
- Two stomachs – proventriculus for chemical digestion and ventriculus for grinding
- Oxynticopeptic cells in stomach produce hydrochloric acid and pepsinogen
- Columbiformes and Galliformes require grit to help grind down hard food
- Biliverdin is the main bile pigment of birds – hence green urates with liver problems
- Cloaca is the common termination of digestive and urogenital tracts

URINARY SYSTEM

This consists only of the kidneys and ureters as, in keeping with weight reduction, birds have no bladder. The ureter terminates in the urodeum of the cloaca.

Kidneys

The kidneys are paired and lie retroperitoneally in the ventral (renal) fossa of the synsacrum. In this region they are intimately associated with the lumbar and sacral plexus nerves and blood vessels that pass through the substance of the kidney itself.

The kidneys are relatively large and extend from the caudal synsacrum cranially as far as the lungs. In most species they are roughly divided into cranial, middle, and caudal parts by the external iliac and ischiadic branches of the abdominal aorta. In passerines the middle portion often appears to be lacking (Johnson, OW 1979). Some species like penguins and herons have a fused caudal kidney in the midline (King & McLelland 1984).

CLINICAL NOTE

The spinal nerves of the lumbar and sacral plexuses run through the kidney parenchyma. This is why many renal conditions like tumors can first present as a lameness problem.

The anatomy of the avian kidney is confusing in comparison to the logical lobule structure of the mammalian kidney (Siller 1983). This is because the avian kidney does not have a distinct demarcation between the cortex and medulla and there is no renal pelvis. Instead the ureter runs along the ventral side of the kidney and branches into collecting ducts that each drain a lobule, consisting of a large area of cortical tissue and a small cone of medullary tissue (Shoemaker 1972). The cortical tissue contains both types of nephron while the medullary cone only contains the loops of Henle, collecting ducts, and the vasa recta capillary network (King & McLelland 1984).

Nephrons

The basic unit is the nephron, as in mammals, but birds show a compromise between reptiles and mammals and have two types of nephron. The cortical nephrons resemble those in reptiles and the medullary nephrons resemble their mammalian counterparts (Johnson, OW 1979; Siller 1971).

Cortical nephrons

These are the most numerous (about 90%) and are confined to the cortical region of the kidney. They excrete uric acid by filtering it through the glomeruli and secreting it into the proximal convoluted tubules. They have no loop of Henle.

Medullary nephrons

These nephrons are also located in the cortical region but have their loop of Henle in the medullary region. It is these that are responsible for forming and concentrating the urine. Birds from arid region tend to have more of these nephrons.

CLINICAL NOTE

As birds have fewer loops of Henle they have decreased ability to concentrate their urine much above blood levels. As a consequence, seabirds, which have a high salt intake, have to rely on extra renal structures called salt glands.

Renal blood supply

The kidneys have a dual afferent blood supply. The high-pressure cranial, middle, and caudal renal arteries subdivide into the afferent glomerular arteries which provide the glomerular filtrate (Johnson, OW 1979). This is influenced by the state of hydration and arginine vasotocin produced from the posterior pituitary gland (Shoemaker 1972).

The external iliac vein, which drains the pelvic limb, branches to form the common iliac vein and caudal renal portal vein (Fig. 6.33). This renal portal vein provides two thirds of the renal blood flow to the kidneys and supplies the proximal convoluted tubules that are responsible for the secretion of urates (King & McLelland 1984; Orosz et al. 1997). Glomerular filtration does not clear urates so it is thought that the renal portal vein plays a significant role in the elimination of these (Siller 1971).

The renal portal system has a unique smooth muscle valve lying at the junction of the common iliac and renal veins (Siller 1983). This has a rich nerve supply and controls the amount of venous blood entering the kidneys. Normally this valve remains closed, allowing venous blood from the hind-limbs and pelvic region to enter the kidney and take part in tubular secretion and resorption. In emergencies, high sympathetic activity stimulates the release of adrenaline (epinephrine), which opens the valve to divert blood away from the kidney to the heart and brain (Johnson, OW 1979; Siller 1971). This can take three routes: first via the open valve directly into the caudal vena cava; via the cranial portal vein to the internal vertebral venous plexus, or via the coccygeal mesenteric vein to the hepatic portal vein and liver (Akester 1971; Siller 1983; West et al. 1981).

Ureter

The ureters have a branched network throughout the kidney parenchyma, terminating in the collecting ducts of each lobule. These are lined by pseudostratified columnar epithelium, which secretes mucus to help the urates pass down (Siller 1971). It often appears whitish due to the urate content inside. The ureter opens into the dorsal wall of the urodeum as there is no urinary bladder or urethra in birds. Urine and urates reach the cloaca and go by retroperistalsis into the rectum and colon where there is mixing with feces and reabsorption of water. The cloaca therefore plays a role in avian osmoregulation (Johnson, OW 1979; Phalen 2000; Sykes 1971).

Nasal gland

All birds have nasal or salt glands located above the eye that are distinct from Harderian and lacrimal glands. In marine species these are well developed and function as salt glands to enable them to drink seawater and excrete the excess salt. These glands also play a role in water conservation in birds from arid climates (Evans 1996; Maina 1996). They are similar to renal tissue, using a system of countercurrent blood flow to remove salt from the bloodstream and pass it down from the nasal passage to be sneezed out of the nostrils. The ostrich, cormorant, duck, goose, falcon, gull, and penguin all have functioning salt glands. They tend to be absent or vestigial in passerine species (Shoemaker 1972).

CLINICAL NOTE

Nasal glands will atrophy if not exposed to salt so this may need to be provided when seabirds are being rehabilitated back to the wild.

Osmoregulation

Most birds gain water by drinking or eating succulent foods like fruit, nectar or meat. Some birds from arid climates (e.g., the Zebra finch) can produce metabolic water instead and conserve water by producing scant urine (Goldstein 2000). Desert birds produce only 55% water in their excrement whereas birds with plentiful access to water provide 75–90% water (Orosz et al. 1997). They also conserve water by cooling warm air as it passes through the nares.

GENERAL INTEREST

Migratory birds often fly for over 72 hours without drinking. Dehydration is prevented because high altitudes prevent evaporative water loss and metabolic water is produced from fat stores. Flying by night also helps to conserve water when the air is cooler.

Urine

Avian urine is the semi-solid product of the kidneys which, on standing, separates out into a white precipitate (urates) and supernatant fluid (urine). Birds have the ability to concentrate their urine but it is less developed than in mammals. Urine is produced by the glomerular filtrate and 90% is reabsorbed by the tubules (Phalen 2000). Like in mammals, therefore, the major control of urine output is tubular resorption.

CLINICAL NOTE

Prior to egg laying, parathyroid hormone (PTH) demineralizes medullary bone to allow calcium to be deposited in the egg yolk and shell. The excess phosphate is excreted via the kidneys causing diuresis. Hence, many hens become polyuric prior to egg laying.

Uric acid

Birds, like reptiles, are uricotelic meaning they excrete 60% of their nitrogenous waste in the form of chalky white urates. Urea is formed only as a by-product of detoxification in the kidney and, to a lesser extent, in the liver. The excretion of urates requires less water but the main advantage to birds is that the developing embryo in the egg is able to produce an insoluble waste product, leaving the water fraction free to be reabsorbed (King & McLelland 1984; Sykes 1971).

Uric acid is synthesized in the liver and excreted in the kidney by glomerular filtration (10%) but mainly tubular secretion (90%) (Goldstein 2000; Phalen 2000). Urates are also produced independently of urine flow, being secreted by the reptilian-style cortical nephrons and so will still be produced even by very dehydrated birds (Phalen 2000).

Gout

Gout is not a disease but a symptom of hyperuricemia or kidney damage. If the proximal renal tubules are damaged uric acid cannot be excreted, so urate levels rise. As the rate of excretion of urates is relatively independent of glomerular filtration, high levels of urates can be produced even in dehydrated birds. However, if they cannot be flushed out by the kidney they will precipitate causing renal gout. High blood uric acid levels will also cause gout in joints and organs such as the kidneys, spleen, and pericardium (Fig. 6.58).

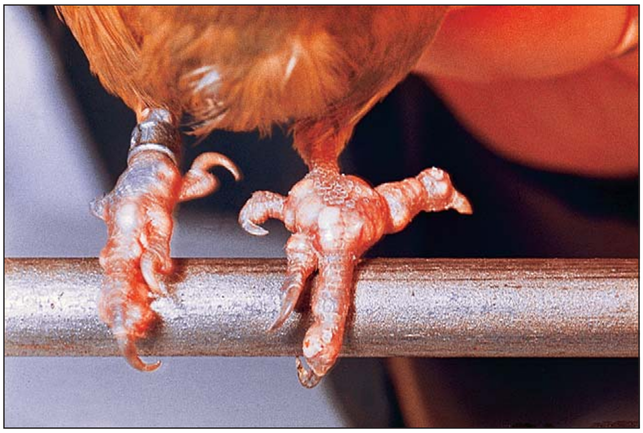


Figure 6.58 • Articular gout in a budgie showing dorsal nodules of white crystalline tophi.

CLINICAL NOTE

Dehydration in birds is serious as it can rapidly lead to irreversible gout. Urea levels can be monitored to estimate dehydration, but 70% of the kidney needs to be damaged before you get elevated blood uric acid levels. Carnivorous birds like birds of prey must also be fasted for 24 hours to avoid false positives.

ADAPTATIONS MADE BY BIRDS IN ARID ENVIRONMENTS

- Kidneys have more medullary nephrons to concentrate urine (Johnson, OW 1979)
- Salt glands excrete excess sodium
- Absorption from coprodeum and colon
- Vascular network in nasal cavity (rete mirabili) to cool incoming air
- Behavioral adaptation

KEY POINTS

- No renal pelvis or bladder
- Dual afferent blood supply
- Two forms of nephron – cortical and medullary
- Uricotelic – production of urates excreted by renal portal system
- Nasal salt glands in marine species
- Production of urates means even mild dehydration or renal damage predisposes to gout

REPRODUCTIVE SYSTEM

Reproduction in the bird follows a definite breeding cycle that is controlled by environmental factors like photoperiod, food availability, and temperature. In temperate climates the trigger factor is the increasing daylight of spring whereas in arid climates the advent of the rainy season bringing increasing food supplies stimulates the gonads to develop (Millam 1997). In order to minimize weight the gonads enlarge for the breeding season and become small and dormant at the end of the season (Evans 1996). In some species this can be dramatic; for example, the gonads of the starling (*Sturnus vulgaris*) increase 1500 times in size during the breeding season (Maina 1996).

The pineal gland is thought to be the center of the complex reproductive and migratory avian clock. However, the main detector of increasing daylight lies not in the eyes or pineal gland but in the hypothalamus. Here photoreceptors release gonadotropin-releasing hormone (GnRH) via the bloodstream to the pituitary gland. In birds two forms of GnRH are released but the exact demarcation of functions is still under research (Millam 1997). This then stimulates the production of follicle-stimulating hormone (FSH) and lutropin luteinizing hormone (LH), which trigger gonadogenesis and breeding (Kirby & Froman 2000).

Once breeding is finished the shorter days of summer stimulate resorption of gonadal tissue and allows time for molting. Under the influences of prolactin and the pineal gland migratory species lay down fat and increase food intake. The short days of winter then inhibit the gonads, allowing them to be stimulated again in the spring.

Birds differ from mammals in that the female is heterogametic, being ZW, and the male is homogametic, being ZZ. This means the sex of future offspring is decided after ovulation and not after fertilization.

SEXING BIRDS

Many birds and especially psittacines are monomorphic, making it difficult to distinguish gender. The following methods can be used:

- External secondary sexual characteristics – Fowl have some useful sex-linked color/feather traits exploited by commercial chicken farms for rapid sexing. Male budgies have a blue cere (Fig. 6.59) while the hen has a brown cere. The male Eclectus parrot is vivid green but the hen is mainly red.
- Vent sexing – This was the traditional method used in poultry farming. Day old chicks were sexed by everting the lip of the vent to expose this tiny genital region. This appears rounded in the male chick and conical in females.
- Surgical sexing – This involves direct visualization of the gonads by laparoscopy into the left abdominal airsac under anesthetic.
- DNA analysis of blood.

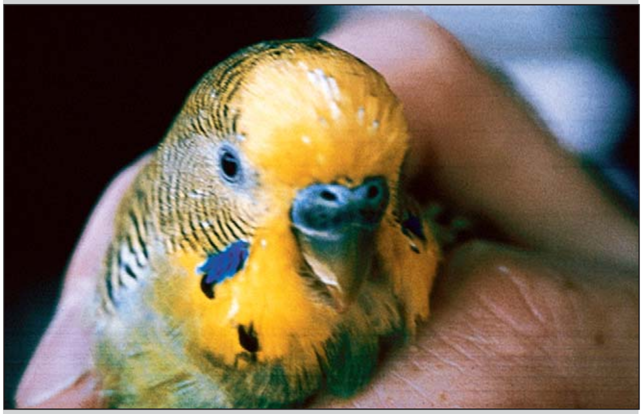


Figure 6.59 • Cock budgie (*Melopsittacus undulatus*) showing blue cere.

Male

Testes

The bean-shaped testes are paired and lie near the cranial pole of the kidney, just caudal to the adrenal glands. Medially, the testes lie close to the aorta and the caudal vena cava. Each testicle is suspended by a short mesorchium and is surrounded medially by the abdominal airsac. The left testis tends to be larger than the right in immature birds (King & McLelland 1984) (Fig. 6.60).

The testes are under the influence of FSH and LH and the dimensions can increase dramatically with sexual activity. In the non-breeding season the testes shrink to almost nothing and may be hard to visualize. The dormant testes

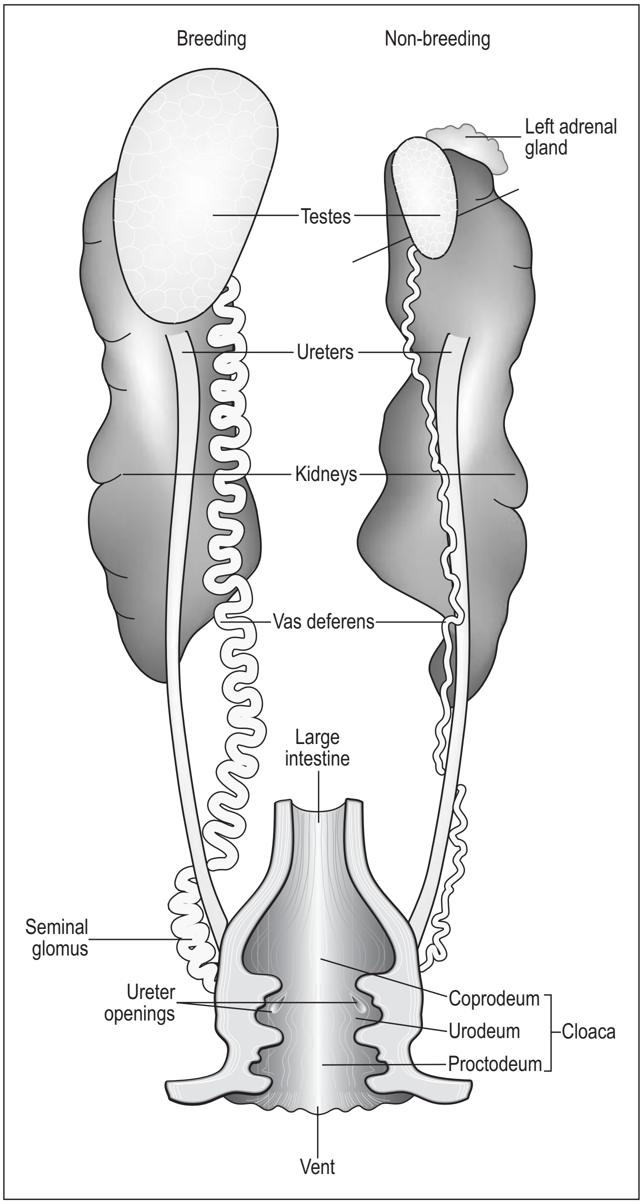


Figure 6.60 • Ventral view of male passerine urogenital tract. The right side shows the large breeding testes and seminal glomus while the left side shows the dormant non-breeding testes.

are light brown to yellow in color, turning white when the bird becomes sexually active. In some psittacine species, like cockatoos (*Cacatua* spp.) and macaws (*Ara* spp.), the immature or dormant testes can even appear black due to melanocytes located in the interstitium of the testes.

The testes consist of seminiferous tubules, which produce the sperm from the epithelium. The interstitial or Leydig cells lie meshed between the seminiferous tubules and, under the influence of LH, produce the main androgens: testosterone and androstenedione (Kirby & Froman 2000; Lake 1981). These hormones provide the secondary sex characteristics like coloration and song during courtship.

The tunica albuginea is much thinner than in mammals and there is no pampiniform plexus. The epididymis is smaller and less developed as sperm maturation occurs in the vas deferens and not, as in mammals, in the epididymis. The vas deferens is closely associated with the ureter in the dorsomedial midline celom but is distinguished from it by its zig-zag appearance. It enters the dorsal wall of the urodeum. There are no accessory sexual glands.

CLINICAL NOTE

In domestic fowl the epididymis has an appendix which attaches by connective tissue into the ventral part of the adrenal gland. Surgical castration is therefore not always permanent because in castrated males this area of tissue can sprout nodules that secrete androgens (King & McLelland 1984).

HOW CAN SPERM DEVELOP AT THE HIGH AVIAN TEMPERATURE OF 40–42° C?

- Most spermatogenesis occurs in the early hours of the morning when temperatures are coolest.
- The adjacent abdominal airsacs may play a role in cooling (Maina 1996).
- In passerines, which have the highest body temperatures, the vas deferens elongates distally to form a cloacal promontory called the *seminal glomus*. This is the main site of sperm storage and functions like a scrotum in keeping the sperm at temperatures 4° C lower than the core temperature. The seminal glomus projects into the cloaca and helps sexually differentiate these species during the breeding season (Lake 1981; Orosz et al. 1997).

Phallus

When present, the avian phallus is solely reproductive and becomes engorged by lymph fluid instead of blood during erection (Kirby & Froman 2000). Owing to the lack of accessory sex glands, avian semen has low volume (e.g., the cockerel has an ejaculate of only 0.5–1 ml) but some lymph may contribute to the seminal fluid (Lake 1981). Sperm remains viable in the female tract for much longer than in mammals and may survive for 5 or 6 days.

Absence of phallus

Psittacines, passerines, pigeons and birds of prey all have no phallus. These species copulate by transferring semen from the everted cloaca directly into the female oviduct (King, AS 1981b).

Non-protrusible phallus

A rudimentary non-protrusible phallus is seen in male turkeys and chickens and lies on the ventral lip of the vent. It consists of a small median tubercle intimately associated on each side with lymphatic folds and vessels. When erected with lymph the phallus develops a median groove which permits passage of ejaculate down into the everted female oviduct (King, AS 1981b; King & McLelland 1984).

Protrusible phallus

The protrusible phallus is elongated and capable of true intromission into the female cloaca and is seen in ratites and Anseriformes. The latter have a curved fibrous phallus that conveys semen via a spiral groove. The distal end lies enclosed in a cavity on the floor of the cloaca and becomes engorged with lymphatic fluid (Fowler 1986; King, AS 1981b).

KEY POINTS

- Size and color changes between dormant and active testes
- Epididymis less well developed. Its close connection to adrenal gland in chickens makes permanent castration difficult
- Seminal glomus used for sperm storage in passerines
- Most birds lack a true phallus

Female

The female embryo has two gonads but only the left one develops, leaving the right ovary and oviduct to regress. This can be identified as a strand of tissue on the right side along the ventral side of the caudal vena cava (Gilbert 1979). As in the male, the female organs regress dramatically after the breeding season (King & McLelland 1984).

CLINICAL NOTE

The right ovary is sometimes retained in birds of prey, although it is rare for it to have a functional right oviduct. Other species like the Common kiwi (*Apteryx australis*) have been known to have two ovaries (Gilbert 1979; King & McLelland 1984).

Sexual maturity

Most domestic fowl come into lay at around 5 months. Seasonal birds will lay in the first spring after hatching. Japanese quail (*Coturnix coturnix*) become sexually active at 5–6 weeks, which is why they are often used in laboratory research.

In ducks, geese, and swans the oviduct is covered by a small membrane where it opens into the urodeum, until the bird reaches sexual maturity. This can be used to distinguish juvenile from mature birds.

Ovary

The left ovary lies caudal to the adrenal gland and near to the cranial tip of the kidney. It consists of a vascular medulla, with nerve fibers and smooth muscle, and a peripheral cortex. It is suspended by the mesovarium and receives its blood supply from the cranial renal artery.

The ovary resembles a bunch of grapes due to large follicles in sexually active hens (Gilbert 1979). The follicle is suspended by a stalk containing smooth muscle that has a rich vascular and nerve supply.

CLINICAL NOTE

The cranial renal artery is very short, making ovariectomy very difficult and bringing a high risk of hemorrhage. Prevention of excessive egg laying is done instead by removal only of the oviduct (salpingohysterectomy) (Orosz et al. 1997).

Oviduct

The oviduct occupies the left dorsocaudal side of the celomic cavity (Fig. 6.61). It is a long coiled tube suspended by the mesosalpinx. The wall consists of ciliated epithelial lining, glands, and smooth muscle. The smooth muscles are thickest in the uterus and vagina to aid with sperm transport. It is divided into five parts: the infundibulum, magnum, isthmus, shell gland (uterus), and vagina (Gilbert 1979; King & McLelland 1984).

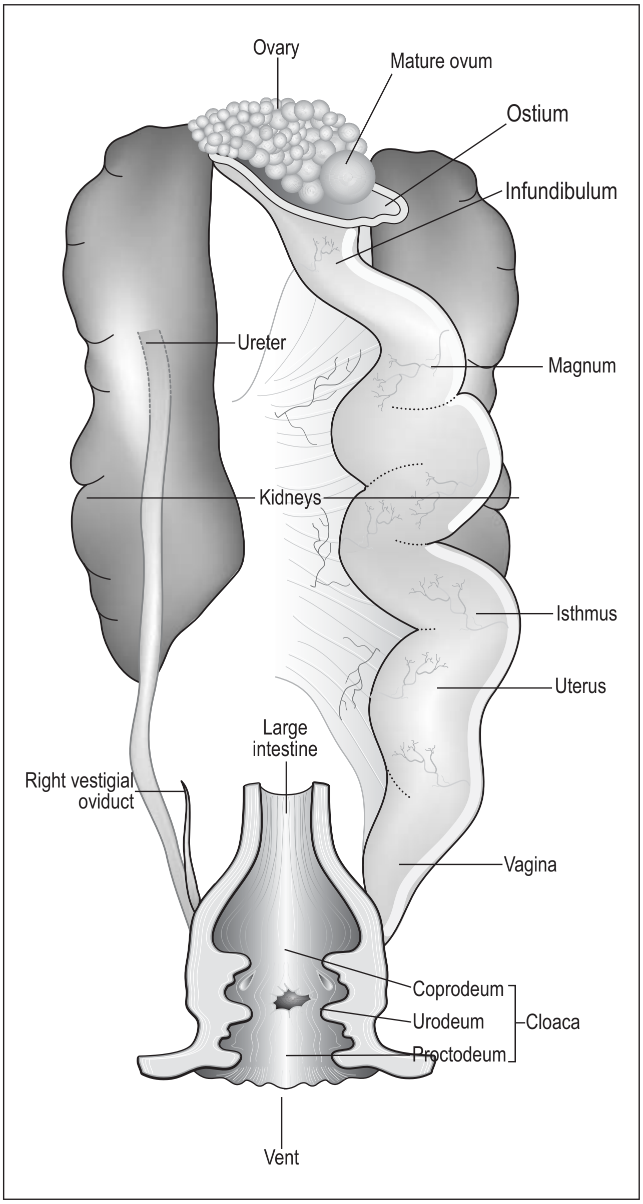


Figure 6.61 • Ventral view of female urogenital tract showing left oviduct and kidneys.

Infundibulum

Unlike mammals, fertilization is not a prerequisite for egg formation and development. The funnel of the infundibulum catches the egg, and fertilization must take place here before the oocyte gets surrounded by albumin (Johnson, AL 2000). Penetration by sperm usually occurs within 15 minutes of ovulation. A thin and dense layer of albumin is then added in the tubular section to surround the yolk. Some species have a sperm host gland in this area to store sperm for a variable time, for later fertilization.

Magnum

The magnum is the longest part of the oviduct; it is coiled and numerous tubular glands give it a thickened appearance. These glands produce the egg white protein albumin, which gives the lumen a milky white color. Calcium, sodium, and magnesium are also added here.

Isthmus

The isthmus divides the magnum from the uterus and is present in poultry but not in psittacines (Orosz et al. 1997). The folds are less prominent than the magnum but its gland secretes more albumin.

Uterus

This holds the egg during shell formation and the majority of time (80%) is spent here (Gilbert 1979). The uterus is very vascular to aid with calcium deposition.

Vagina

The vagina is separated from the uterus by a vaginal sphincter. The smooth muscle here is more powerful than the rest of the oviduct. In some species the egg can remain here for hardening before the egg passes out of the oviduct into the urodeum.

Sperm host glands are in the uterovaginal junction where sperm can be stored for many months, which is why female birds can be fertile weeks after the absence of the male (Johnson, AL 2000).

Endocrine control

In females FSH is mainly responsible for follicular growth. The developing follicles produce estrogen from the theca and interstitial cells, and progesterone from the granulosa cells. Increasing levels of estrogen stimulate a LH surge and, under the influence of this, the follicle splits to release the primary oocyte. Estrogen also mobilizes calcium from the bone, increasing plasma calcium for egg formation.

Progesterone continues to be secreted to inhibit further ovulation and stimulate behavioral changes associated with broodiness and incubation. Prolactin stimulates the production of crop milk in both male and female pigeons. Oviposition in birds is controlled by prostaglandins and arginine vasotocin/oxytocin.

Ovulation

The number of ovulations varies with the species but most wild birds lay only one clutch a year. The infundibulum catches the oocyte and this is facilitated by the left abdominal air sac, which tightly encloses the ovary (Gilbert 1979). However, if the sequence gets out of phase oocytes can be lost into the celom. Some of these will get absorbed but others may cause egg peritonitis. Once ovulation has taken place the follicle shrinks and regresses. No corpus luteum remains as there is no developing embryo to maintain.

GENERAL INTEREST

The avian primary oocyte is the largest animal cell.
The oocyte of the now extinct Madagascar Elephant bird (*Aepyornis maximus*), thought to be the origin of the mythical Roc, had a diameter of 37 cm, and the volume of a bucket!

Egg formation

In the chicken the developing egg travels down the oviduct in about 25 hours, but it takes about 48 hours in psittacines. Protein and lipid are synthesized in the liver and travel to the oocyte in the ovary where they are made into yolk (vitellogenesis). In the infundibulum a thin layer of albumin is laid down during the short 15 minute passage. It takes 3 hours to go through the magnum where it acquires albumin, sodium, calcium, and magnesium.

In the isthmus the inner and outer shell membranes are formed and calcification begins. The last 20 hours are spent in the uterus where the shell is formed and the albumin doubles in volume, creating the “plumping effect”. During the last 15 hours the highly vascular uterus draws calcium rapidly from the blood. The completed egg then passes through the vagina in seconds to be expelled from the vent (King & McLelland 1984).

Oviposition

Expulsion of the egg involves contraction of the uterus (shell gland) with relaxation of abdominal muscles and can take from a few hours to minutes. Cuckoos have the ability to lay their small eggs in a few seconds so they can get away before the host returns (Gilbert 1979; King & McLelland 1984). Contraction of the uterus is thought to be controlled by a combination of vasotocin/oxytocin and prostaglandins (Johnson, AL 2000).

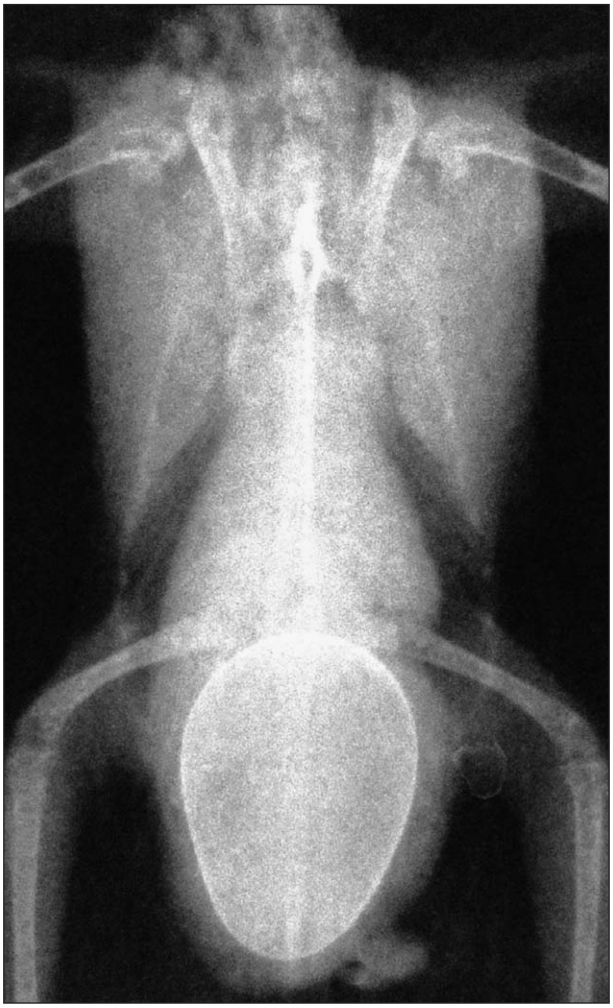


Figure 6.62 • Ventrodorsal radiograph of eggbound budgie with increased radiopacity of the pelvic limbs. In laying birds calcium is laid down in the medullary cavity prior to laying in a phenomenon called *polyostotic hyperostosis*. This bird also has an enlarged hepatic silhouette most likely due to hepatic lipidosis.

CLINICAL NOTE

Prostaglandins are of more use clinically for treatment of egg-bound birds because they not only cause contraction of the oviduct but relax the uterovaginal sphincter.

Post egg laying

The bird enters the non-breeding state while it is incubating and caring for its brood. The resting ovary has a shrunken appearance similar to a juvenile ovary and the oviduct regresses into an inconspicuous, narrow tube.

GENERAL INTEREST

The Red jungle fowl can lay eggs indeterminately and can quickly lay more if eggs are lost from the clutch. Domestic fowl have been bred from this species and this is why they can lay eggs almost daily for up to 352 days per year.

Avian eggs

Avian eggs differ from reptilian eggs in that the principal stored nutrients are fats in the yolk sac. This produces more energy and water than protein and allows birds to survive in more arid environments. They are also porous to allow for gas exchange. The size of the egg varies with the type of newborn: altricial species lay much smaller eggs than precocial ones.

The egg consists of a germinal disc, yolk, yolk membranes, albumin, and shell (Fig. 6.63). The germinal disc is either a blastoderm (fertilized) or blastodisk (unfertilized). The yolk is thick and viscous and forms the main nutrient for the embryo. White yolk is mainly protein with some fat while yellow yolk is the reverse. The yolk membranes form a barrier between yolk and the albumin but it is permeable to water and salts.

The albumin is less viscous than the yolk and composed mainly of protein. A thin layer of albumin encloses the yolk membranes and this suspends the yolk in the center of the egg by twisted strands called chalazae.

The shell consists of the shell membranes, the testa and the cuticle. The testa is the main thickness of the shell and consists of a matrix of fibers and calcium carbonate. The cuticle is water repellent and acts as a barrier to infection. In contrast to reptile eggs, avian eggs can be pigmented by two pigments, porphyrin and biliverdin, which are deposited throughout the testa. Small flaws between the calcium carbonate crystals form pores which allow the egg to breathe (Gilbert 1979; King & McLelland 1984).

Chicks

Chicks fall into two categories: precocial (nidifugous) and altricial. The precocial chicks have natal down, hatch with their eyes open, and can survive outside the nest within 1or 2 days (Fig. 6.64). In contrast, altricial chicks are born blind and naked and require long periods of feeding.

KEY POINTS

- Birds have only a left ovary and oviduct.
- Sperm storage is possible in sperm glands in the oviduct.
- Oviposition is controlled by prostaglandins and oxytocin/vasotocin.
- Avian eggs differ from those of reptiles in that they can be pigmented, are more porous, and the principle nutrient to the embryo is egg yolk.
- Young can be either precocial or altricial.

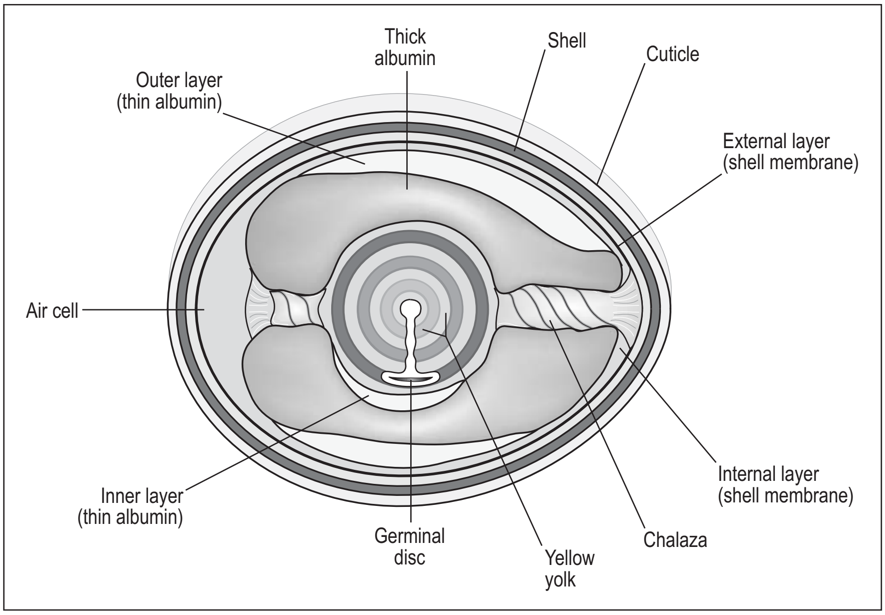

Thick albumin
Shell
Cuticle
Outer layer (thin albumin)
External layer (shell membrane)
Air cell
Internal layer (shell membrane)
Inner layer (thin albumin)
Germinal disc
Yellow yolk
Chalaza

Figure 6.63 • Internal structure of the egg.

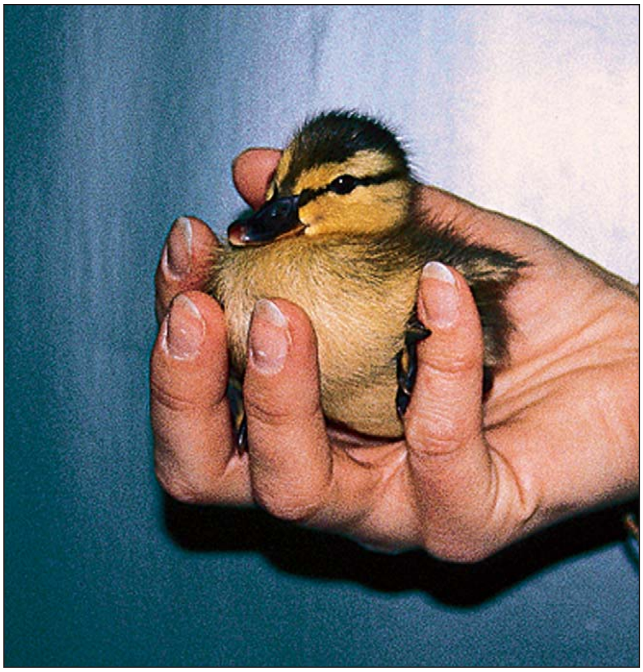


Figure 6.64 • Precocial (nidifugous) chicks are born with natal down and their eyes open and can survive outside the nest within 1–2 days.

ENDOCRINE SYSTEM

Pituitary gland

The pituitary gland or hypophysis is a small organ lying attached to the ventral part of the brain stem, just caudal to the optic chiasma. There are two lobes. The anterior lobe (adenohypophysis) secretes thyroid-stimulating hormone (TSH), adrenocorticotropic hormone (ACTH), FSH, and LH, which regulate the action of the thyroid, adrenals and gonads (see Reproductive system for discussion of the gonads). It also produces prolactin, melanocyte-stimulating hormone (MSH), and somatotropin. FSH and LH are produced under the action of GnRH from the hypothalamus (Oglesbee et al. 1997).

FSH in the male bird increases testicle size and stimulates spermatogenesis; in females it stimulates estrogenesis and development of the ovarian follicles. LH stimulates the Leydig cells to produce testosterone in males and in the female it is known to be involved in ovulation. Somatotropin appears to regulate body growth in young birds while ACTH controls the adrenal corticosteroids. TSH controls the thyroid glands; the exact role of the hormone MSH is unknown (Hodges 1981).

Prolactin is involved both in the reproductive system and carbohydrate metabolism. It stimulates brooding and nesting behavior in both males and females and inhibits gonadal activity by suppressing the secretion of FSH and LH. In Columbiformes it stimulates the production of crop milk from the crop epithelium. It is also thought to be associated with premigratory behavior stimulating hyperglycemia and hepatic lipidogenesis (Hodges 1981; King & McLelland 1984).

CLINICAL NOTE

The pituitary should be carefully evaluated in post mortems on budgies as pituitary adenomas and carcinomas are common. A normal pituitary gland measures 2 mm in diameter, but if neoplastic it can be increased 10-fold. Clinical signs caused by hormonal imbalance include persistent hyperglycemia and polydipsia or polyuria, while blindness, exopthalmos, and convulsions can be caused by pressure of the tumor (Rae 2000).

Posterior pituitary

Vasotocin and oxytocin are produced in the hypothalamus and stored in the neurohypophysis or posterior pituitary gland. They act on the uterus and the kidney. Vasotocin plays a major role in body water balance (antidiuretic hormone) and is transported via the bloodstream to the kidney where it causes water resorption. Both hormones play a role in uterine (shell gland) contraction and oviposition, although vasotocin is much more potent.

Pineal gland

This is a conical, pink structure located between the cerebral hemispheres and the cerebellum. This gland is believed to be involved with circadian rhythms, reproductive control, and photoreception (Hodges 1981).

Thyroid gland

These paired, oval glands lie just cranial to the thoracic inlet, lateral to the trachea and medial to the jugular veins. Unlike mammals, birds do not have C cells that produce calcitonin. This is produced instead by the ultimobranchial bodies. Avian thyroglobulin has a higher percentage of iodine than mammals, which is why many birds easily develop iodine deficiency (Oglesbee et al. 1997).

The two hormones thyroxine (T4) and triiodothyronine (T3) play many roles in avian species. These hormones regulate molting by stimulating the growth of new feathers. They also control metabolism, regulation of heat and growth, the reproductive organs, and increasing egg production (Hodges 1981; King & McLelland 1984; Rae 2000).

CLINICAL NOTE

Many birds like the budgie easily become deficient in iodine. This can cause swelling of the thyroid glands called goiter, which can get so large it blocks the esophagus causing regurgitation. In budgies the normal thyroid is pale and should be 2 mm in diameter; any enlargement seen on post-mortem could be a sign of an iodine-deficient diet (Evans 1996; Rae 2000).

Parathyroid glands

These lie caudal to the thyroid and consist of two pairs of small, yellow glands, which are often fused together. These glands secrete PTH which, as in mammals, controls calcium and phosphorous metabolism. It raises serum calcium by both increasing calcium reabsorption from the kidney tubule and releasing it from bone via osteoclastic activity. It decreases phosphorous levels by decreasing tubular reabsorption (Hodges 1981; Rae 2000).

As some birds, like the domestic, can lay almost one egg daily they have a much higher demand for calcium than mammals. Estrogen stimulates the deposition of calcium in the medullary cavity of bones about 10 days prior to laying (Fig. 6.62). Under the action of PTH this calcium deposit is then shifted from the medullary cavity into ionized plasma calcium and used to calcify the eggshell (King & McLelland 1984; Oglesbee et al. 1997; Rae 2000).

Ultimobranchial bodies

These are small, pink, flattened glands lying just caudal to the parathryoids and consist of C cells, which secrete calcitonin. The role of calcitonin in birds is unknown as it does not appear to lower serum calcium. It may play a role in limiting extensive reabsorption of bone by PTH (Hodges 1981; King & McLelland 1984; Oglesbee et al. 1997).

Adrenal glands

These are small, ovoid glands lying just cranial to the kidneys and gonads on either side of the aorta and caudal vena cava. In birds the cortex is not well differentiated from the medulla (Hodges 1981; Rae 2000). In some male birds, like the domestic fowl, they are firmly attached to the appendix of the epididymis by connective tissue (King & McLelland 1984).

Adrenaline and noradrenaline (norepinephrine) are secreted by the medullary part of the gland. The cortical parts secrete corticosterone and aldosterone. In birds corticosterone has both glucocorticoid and mineralocorticoid activity and so plays a bigger role than aldosterone in electrolyte balance.

Pancreas

This lies in the mesentery of the duodenum and is often divided into three lobes. The endocrine portion has three types of islets: alpha, beta and delta. The alpha cells secrete glucagon, which regulates carbohydrate metabolism, increasing serum glucose levels by gluconeogenesis, lipolysis, and glycogenolysis. The beta cells produce insulin, which lowers the level of serum glucose by stimulating tissue uptake and storage. Delta cells produce somatostatin, which regulates the levels of glucagon and insulin. Birds have much higher glucagon levels and lower insulin levels than mammals (Rae 2000). It is thought that glucagon plays a far higher role in carbohydrate metabolism than insulin (Hazelwood 2000; Hodges 1981; Oglesbee et al. 1997). The role of insulin is still poorly understood (Rae 2000).

Other F cells (sometimes called PP cells) situated in the exocrine tissue of the pancreas secrete avian pancreatic polypeptide. This inhibits gastrointestinal motility and gallbladder and pancreatic secretion. It also induces a sense of satiety via the central nervous system (Hazelwood 2000).

Gastrointestinal endocrine cells

Endocrine cells are scattered along the intestinal epithelium but the majority of endocrine cells are situated in the pylorus. Hormones secreted by the gastrointestinal tract include somatostatin, secretin, and avian pancreatic polypeptide.

KEY POINTS

- Prolactin stimulates broodiness, production of crop milk, and build up of fat stores prior to migration.
- Laying hens deposit calcium in the medullary cavity of bone prior to laying, under the influence of parathormone.
- Birds have a higher iodine requirement than mammals, which is why goiter is common in some birds.
- In birds corticosterone has both a mineralocorticoid and glucocorticoid effect.
- Glucagon plays a bigger role in avian carbohydrate metabolism than insulin.

NERVOUS SYSTEM

The avian brain is small with less development of the cerebral hemispheres. These are composed mainly of the *corpora striata*, indicating that birds use less learning and memory but more instinct and stereotypical behavior. More intelligent birds like parrots have better development of the cerebral hemispheres.

There is a well-developed cerebellum for locomotion and large optic lobes for vision. There are 12 pairs of cranial nerves, as in mammals. The spinal cord resembles that of mammals, having three meninges: the dura, arachnoid, and pia mater. However, as the cord is the same length as the canal there is no cauda equina (King & McLelland 1984). The spinal cord becomes enlarged at the brachial and lumbosacral plexi. Flying birds have a more prominent brachial plexus, while running birds like the ostrich have a large lumbar plexus (Rosenthal 1997a). A unique feature of birds is the "glycogen body." This pea shaped, glycogen-rich cleft lies on the dorsal surface of the lumbosacral plexus but its function is unknown (Rosenthal 1997a).

The roots of the lumbar plexus are in contact with the dorsal surface of the cranial kidney; the sacral plexus is totally embedded within its middle division. Some of the roots of the pudendal plexus are embedded in the caudal division.

Senses

The fact that birds fly mean they must have good aerial vision, but olfaction is less essential due to the absence of odors in the sky. Hence, in the avian brain the olfactory bulbs are reduced while the optic lobes are increased. Recognition of food relies mainly on sight and, to a lesser degree, by feel (ducks and geese) and smell.

Sight

The large eyes and well-developed optic lobes in the brains means birds have excellent vision. In fact, in many species the two eyes weigh more than the brain (Evans 1996; Gunturkun 2000). Most birds also have a high degree of binocular and color vision. The optic nerve is the most developed cranial nerve in birds, being largest in Corvids and Falconiformes and smallest in nocturnal species. There is no consensual light reflex in birds because there is complete decussation of the optic nerve fibers at the optic chiasma (King & McLelland 1984).

External adnexa

Although the eyelids are open and well developed in precocial birds, they are sealed in altricial birds. Eyes usually open between 2 and 4 weeks and usually take a few days for full separation.

Birds have upper and lower eyelids and a nictitating membrane. The lower lid is far more mobile and covers more of the eye while blinking than the upper (Martin 1985). Modified feathers, called filoplumes, are on the lids and act like mammalian cilia.

The lids close mainly in sleep. Blinking is performed mainly by the mobile nictitating membrane (30–35 times per minute in domestic fowl). This is usually transparent in diurnal species so that vision is not impaired.

Orbital glands

The Harderian gland is the largest. It lies craniomedial within the orbit behind the nictitating membrane and produces a mucoid secretion that moistens the cornea. The lacrimal gland lies at the caudolateral margins. Both glands empty via dorsal and ventral puncta into the nasolacrimal duct. The nasal (salt) gland lies dorsomedial to the orbit and empties separately into the nasal cavity (Martin 1985).

Globe

The eyeball consists of a small, unprotected anterior portion covered by the cornea, and the posterior part that is protected by the two orbits separated by a thin bony septum. The anterior part has three basic shapes: flat, globose or tubular, depending on the species (Figs. 6.65 and 6.66, Table 6.5). The shape of the eyeball is formed by 10 to 18 scleral ossicles, which are visible by radiography (Fig. 6.67). These are a ring of overlapping bones, which strengthen the eye and provide an attachment for the ciliary muscles, permitting greater accommodation (Martin 1985). They are largest in owls and diurnal raptors and less developed in Psittaciformes and Anseriformes.

The eyeball fills the orbit so the extraocular muscles are less developed than in mammals (Kern 1997; Martin 1985). The single occipital neck joint and long, flexible neck compensate instead by allowing the bird to rotate its neck. Movements of each eye are independent of each other.

Iris

This is usually dark in color, ranging from brown to black, but in owls it can be bright yellow and it is pale blue in gannets. It can also vary with diet as it contains lipid droplets. In some species it can help identify age; for example, the African Gray parrot has a gray iris when juvenile that becomes yellow when mature. In contrast to mammals, the muscles are striated, making them under some voluntary control, so atropine will be ineffective (Fig. 6.68). Dilation of the avian iris is only effective with mydriatics such as the muscle relaxant vecuronium.

CLINICAL NOTE

The pupil is round and, as the iris has striated muscle, it cannot be dilated with normal mydriatics. There is no consensual light reflex (Fig. 6.68).

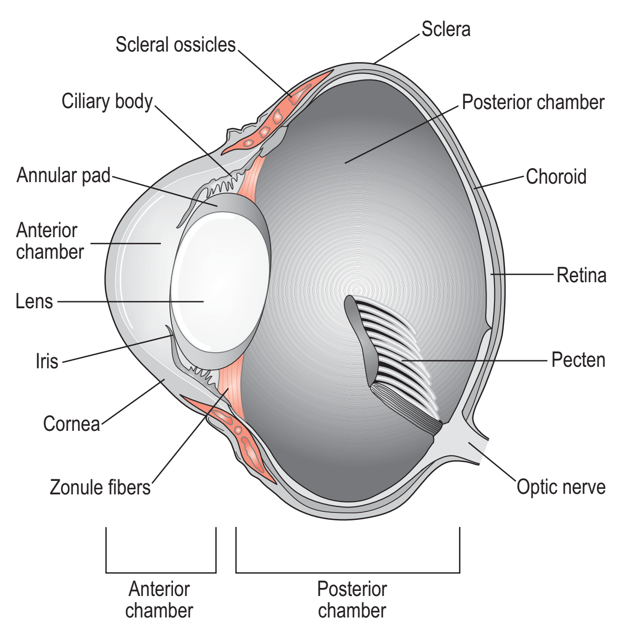


Figure 6.65 • Cross-section of avian eye showing small, unprotected anterior portion covered by the cornea and large posterior part with pecten. The intermediate area is supported by a ring of scleral ossicles.

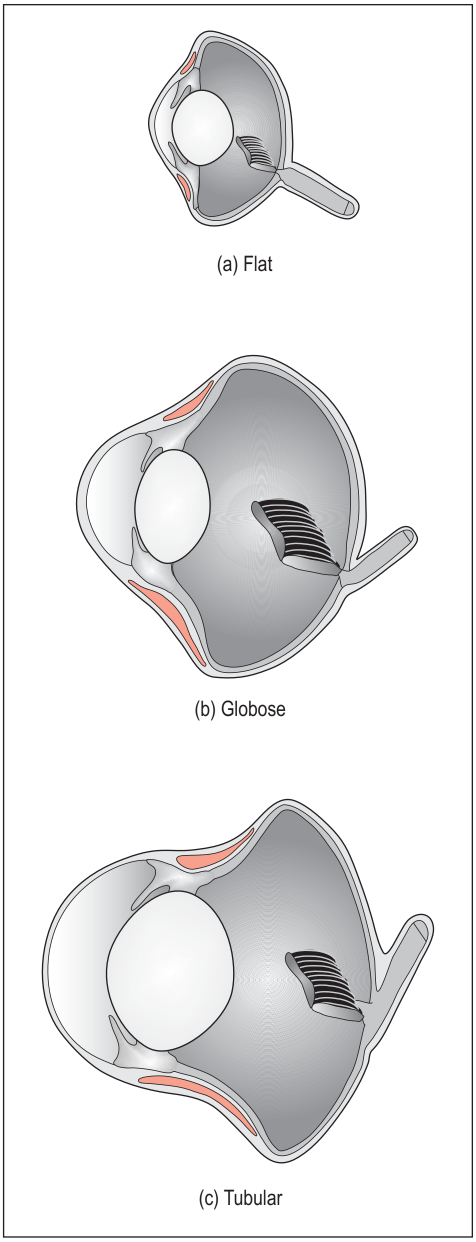


Figure 6.66 • The anterior part of the avian eye has three basic shapes depending on species.
(a) Flat
(b) Globose
(c) Tubular

Table 6.5 Basic avian globe shapes (King & McLelland 1984)

Globe shape	**Species**	**Vision**
Flat	Most birds e.g., Chicken	Poor visual acuity
Globose	Birds of prey, Passerines	Good visual acuity
Tubular	Nocturnal birds of prey	Excellent visual acuity

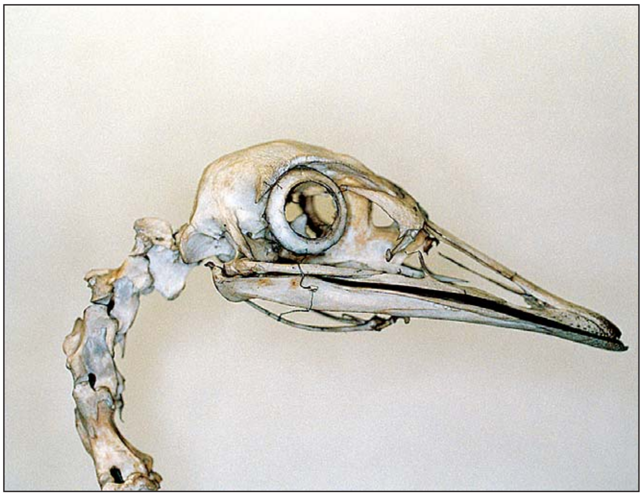


Figure 6.67 • Skull of rhea (*Rhea americana*) showing ring of scleral ossicles.

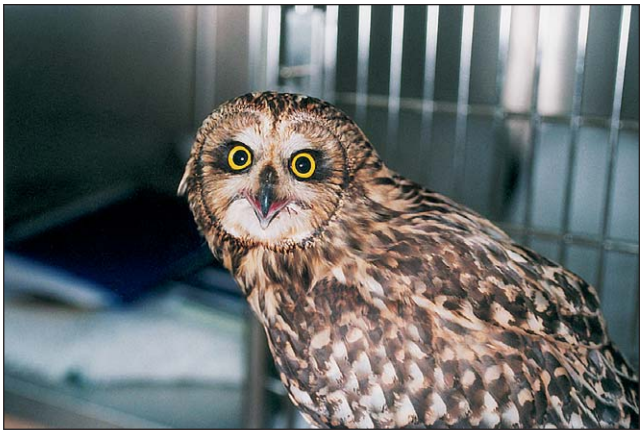


Figure 6.68 • Birds have round pupils and the iris has striated muscles which cannot be dilated with normal mydriatics like atropine.

Lens

Accommodation is very well developed in birds, with a softer lens to allow for rapid accommodation. There are three mechanisms for this. Diurnal birds use the posterior sclerocorneal muscles to compress the lens while nocturnal birds and hawks use the anterior sclerocorneal muscle. In diving birds the cornea has poor accommodation underwater so they use the combined action of sclerocorneal muscles and the iris sphincter muscle.

Retina

In order to attain high visual acuity, the avian retina lacks blood vessels and tapetum lucidum to prevent shadows and scattering of light. Instead, it is vascularized by a black, vascular comb-like structure called the pecten. This structure extends from the optic disk into the vitreous body towards the lens and is unique to birds. It appears to nourish the relatively avascular retina, aid in acid–base balance, and facilitate fluid movement within the eye (Gunturkun 2000; Martin 1985).

The fundus is usually gray or reddish. The optic disk is elongated and oval but is mainly obscured by the pecten. Cones, which provide visual acuity and excellent color vision, are more numerous in diurnal species, forming up to 80% in the chicken and pigeon. Nocturnal birds have more rods than cones.

CLINICAL NOTE

Many diurnal birds lack rods so have excellent day vision and poor night vision, which is why dimming the lights makes it easier to catch birds (King-Smith 1971).

Fovea

The fovea is the area of densely packed cone cells and, in birds, is deep for greater visual acuity. Most birds have a central fovea but ground dwellers have none, and Falconiformes, which have the celebrated "eagle eye", have two to allow high visual acuity (Kern 1997; Martin 1985).

Hearing

After vision, hearing is the second most important avian sense. Birds, especially diurnal ones, generally have the same hearing ability as humans. However, nocturnal birds like the owl have an amazingly accurate ability to pinpoint sound, and homing pigeons can hear extremely low frequencies. Some nocturnal and underwater species use echoes to locate obstacles while flying or diving. Birds also have the ability to hear sounds of rapid frequency because the syrinx of songbirds is capable of producing a duet of high pitch inaudible to the human ear.

Like mammals, the ear is the organ of hearing and balance and is divided into the external, middle and inner ear.

External ear

There is no pinna and the external ear opening is hidden by feathers called ear coverts. The surrounding skin is loose and can be drawn forward by the dermo-osseus muscle to reduce the opening to a vertical slit. This flap can also close over to block sound entering the ear, in for example, the crowing cock (King-Smith 1971). In some species, such as owls, a vertical skin flap called the *operculum* lies rostral to the external ear opening (Fig. 6.70). This has a row of stiff feathers at right angles and this facial ruff can be erected by skeletal muscle to help locate sound, equivalent to someone cupping their hands behind their ears. Acute hearing is also facilitated in some owl species by asymmetrical ear positioning, allowing one ear to hear sounds on a horizontal plane and the other on a vertical plane (King & McLelland 1984; Necker 2000).

Middle ear

The middle ear is the air-filled cavity between the tympanic membrane and inner ear. There is only one bony ossicle called the columella (equivalent of the mammalian stapes) which transmits sound vibrations from the tympanum to the vestibular window of the inner ear (Necker 2000). The middle ear is connected to the oropharynx by the pharyngotympanic tubes (the equivalent of mammalian eustachian tubes). As birds need to adjust rapidly to high altitudes, these tubes are short and open directly into the pharynx via the common infundibular cleft (Evans 1996; King & McLelland 1984) (Fig. 6.69).

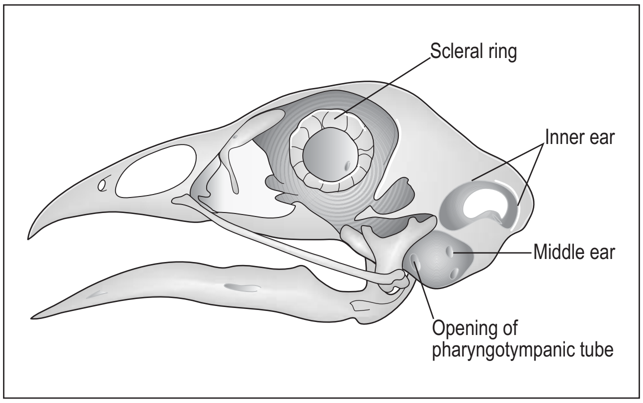


Figure 6.69 • Skull of Domestic fowl (*Gallus gallus*) showing scleral ossicles and location of ears.

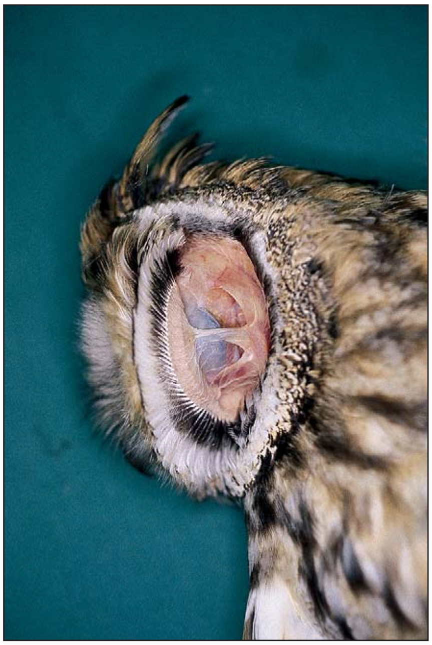


Figure 6.70 • Long eared owl (*Asio otus*) showing the operculum. This is a flap of feathered skin rostral to the external ear opening which can be raised to capture sound on the same principle as a satellite dish.

Inner ear

This contains the organ of hearing (the cochlea) and the organs of balance (the three semicircular canals, utricle, and saccule). Unlike in mammals, the cochlea is short and not coiled and the semicircular canals are larger and more thick walled. The eighth cranial nerve receives both vestibular and auditory sensory fibers.

Olfaction

The olfactory system consists of the external nares and the caudal conchae that are lined by olfactory epithelium and connected to the olfactory bulbs of the brain. There is no vomeronasal organ (Mason & Clark 2000).

Birds do have a sense of smell, although it may not be as highly developed as vision and hearing (King-Smith 1971). Many species use olfactory cues to find food, and smell plays a role in maternal identification of young (Mason & Clark 2000). The olfactory bulbs are smallest in seed eaters and larger in aquatic birds. The ground-dwelling nocturnal kiwi, which eats earthworms, has the largest of all and is the only bird with nostrils at the end of its beak. Vultures, which feed on dead carrion, also have a well-developed sense of smell, and homing pigeons use olfactory cues to find their way home (King & McLelland 1984).

Taste

The taste buds are confined to glandular non-cornified epithelium. They lie at the base of the tongue, and in the roof and floor of the oropharynx. In parrots they lie at either side of the choana and at the rostral end of the laryngeal mound.

The total number of taste buds is far fewer than in mammals, with the chicken having 24 taste buds and parrots 350, in contrast to 9000 in man and 17,000 in the rabbit (Klasing 1998; Mason & Clark 2000). Birds, however, do respond to salts and acids and dislike bitter-tasting substances. They are also far more tolerant of spicy foods than mammals. For example chili red peppers (capsaicin), which would be irritating to mammals, have little effect on birds. Parrots and humming birds have a definite preference for sugary water, while birds with salt glands have a higher preference for salt tastes (King & McLelland 1984; Mason & Clark 2000).

Touch

Birds have widely distributed mechanoreceptors called Herbst corpuscles in their skin. These are located deep in the dermis and found on beaks, legs and associated with feather follicles. In the plumage these are used to ruffle feathers and help stimulate preening.

Avian species that use their beak to search and locate food also have these receptors located in a well-developed "beak tip organ", which is located along the edge and tip of the upper beak in aquatic birds like ducks and geese (Gerlach 1997b). Psittacines have them located in the lower beak. These remarkably sensitive touch receptors compensate for the lack of taste buds. For example, mallard ducks have more sensation in their beak tip than we humans have in our index finger tip (Klasing 1998).

CLINICAL NOTE

Psittacines with beak malocclusion may need the lower beak trimmed, along with the upper, in order to maximize function of the beak tip organ to aid in food prehension.

KEY POINTS

- Birds have excellent hearing and sight but poor sense of smell and taste.
- There is no external ear and only one middle ear bone, called the columella.
- The eyes have scleral ossicles. An avascular retina is nourished by the pecten, and fovea are present for visual acuity.
- There is no avian consensual light reflex.
- The iris is controlled by striated muscle pupil and so is non responsive to atropine.
- Neck rotation compensates for poor orbital muscles. Eyes can, however, move independently.

INTEGUMENT

Avian skin is very thin as it is protected by the plumage and helps to reduce weight (Spearman 1971) (Fig. 6.71). It is lightly attached to underlying muscle but firmly attached to bone. There are only three glands: the uropygial or preen gland, the aural gland and the vent gland. The absence of sweat glands means birds have to lose heat through their skin and by evaporation from the respiratory system.

The epidermis consists of the superficial *stratum corneum*, which contains keratinized dead cells and the deeper living *stratum germinativum*. This layer is thin and fragile under the feathers but thicker on the feet and around the beak in order to resist mechanical stress. A unique feature of the avian epidermis is that it acts like a holocrine sebaceous gland, secreting a thin lipid film that helps in the maintenance of the plumage (Spearman 1983; Spearman & Hardy 1985).

The dermis is composed of connective tissue and contains the feather follicles, nerves and blood vessels. In some species, like the domestic fowl, the dermis becomes thickened and highly vascularized to form combs and wattles, but the epidermis remains thin, making them prone to injury (Dyce et al. 2002). The subcutaneous layer is mainly composed of loose connective tissue and some adipose tissue. It is here that fat is laid down in aquatic species like ducks, geese, and swans, and prior to migration in migratory species (King & McLelland 1984).

CLINICAL NOTE

Avian skin is very thin and, owing to the scant subcutaneous tissue, very inelastic. Handle tissues with care when suturing and avoid excess skin tension as it tears easily. Owing to the fact that it has less blood and a smaller nerve supply than mammals, skin wounds bleed less and are less sensitive.

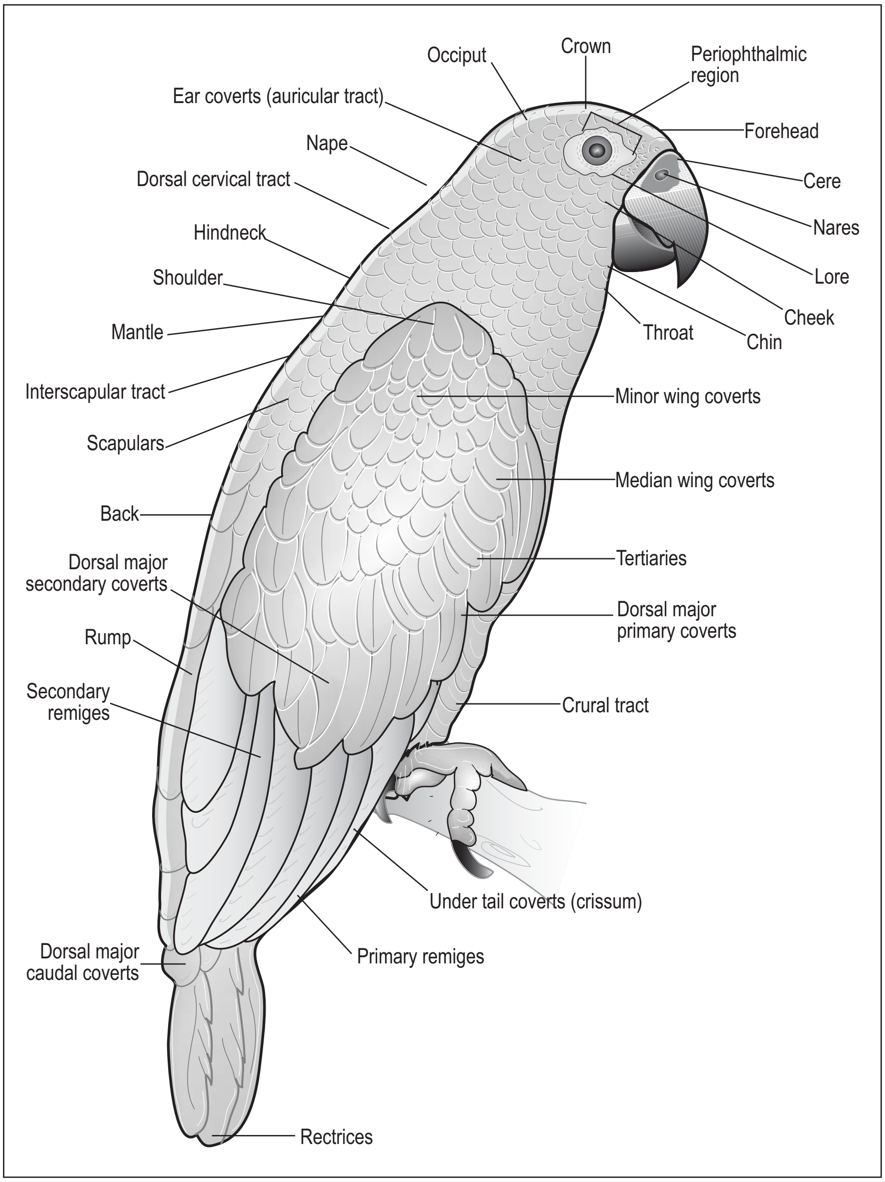

Occiput
Crown
Periophthalmic region
Ear coverts (auricular tract)
Forehead
Nape
Dorsal cervical tract
Cere
Nares
Hindneck
Lore
Shoulder
Cheek
Mantle
Throat
Chin
Interscapular tract
Minor wing coverts
Scapulars
Median wing coverts
Back
Tertiaries
Dorsal major secondary coverts
Dorsal major primary coverts
Rump
Crural tract
Secondary remiges
Under tail coverts (crissum)
Primary remiges
Dorsal major caudal coverts
Rectrices

Figure 6.71 • Avian plumage.

Uropygial gland

The uropygial gland is the preen or oil gland and is found at the dorsal base of the tail (Evans 1996) (Figs. 6.72 and 6.73). It is most developed in waterfowl and maintains feather condition and waterproofing. It also acts as a bacteriostat (Spearman 1983). It is a bilobed holocrine gland drained by a papilla dorsocaudally and is covered by a tuft of down feathers called the uropygial wick. This feather tuft may aid in transmitting oil from the gland to the beak while preening (Dyce et al. 2002; Spearman & Hardy 1985). This gland is prominent in African Grays and budgies but absent in many parrots (e.g., Amazon parrots), ostriches and many pigeons (Bauck, Orosz & Dorrestein 1997; Bezuidenhout 1999; Evans 1996; Spearman 1971).

Lipid secreted by this gland and the epidermal cells are spread over the feathers by the bill during preening (Spearman 1983). This lipid layer forms a protective bacteriostatic layer over the skin and may explain why birds are less prone to skin infections. Birds can preen as often as once an hour at rest (Bauck, Orosz & Dorrestein 1997).

Aural sebaceous glands around the external ear secrete a waxy substance. Vent glands secrete mucus but their function is unknown, although it may be linked to internal fertilization.

Podotheca

The non-feathered area of the legs is called the *podotheca* and is composed of keratinized epidermal plates called scales. The skin is thickened in the ventral metatarsophalangeal region and is designed to withstand impact on landing. In aquatic species, the skin is softer and more flexible and modified between the toes into webs. The distal phalanx is keratinized into the nail or claw. The dorsal aspect grows

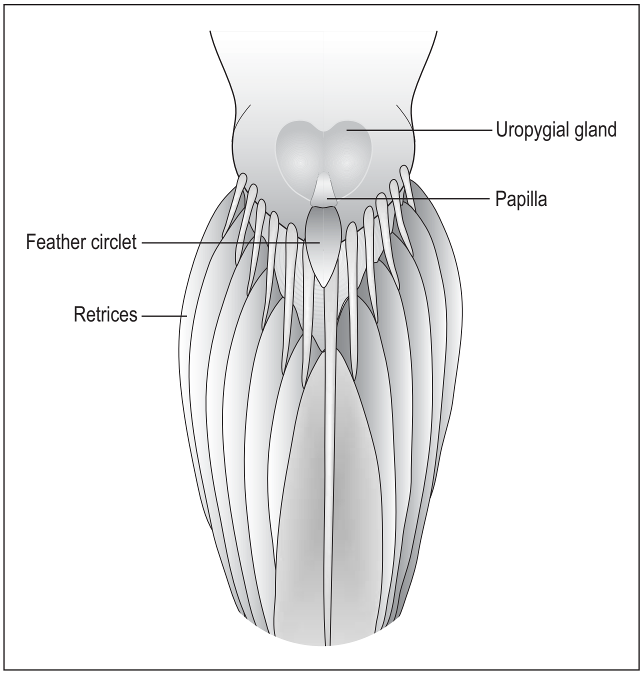


Figure 6.72 • Dorsal view of uropygial gland. Surrounding feathers have been plucked for better visibility.

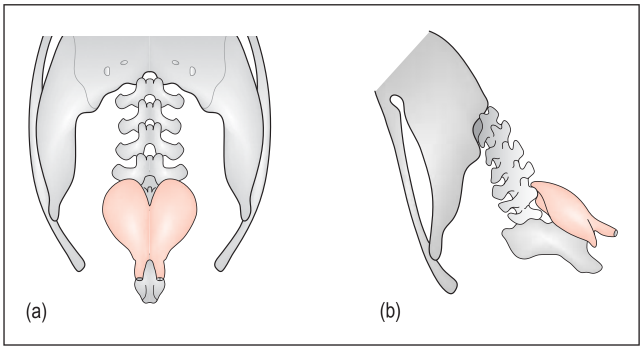


Figure 6.73 • Location of uropygial gland in relation to pygostyle.
(a) Dorsal view
(b) Lateral view

faster than the softer ventral side and this gives the claw its curved appearance (Bauck, Orosz & Dorrestein 1997; Spearman 1971; Spearman & Hardy 1985).

Patagia

Patagia are thin membranous sheets of skin located where the wings, neck, and legs join the body. They can be a useful site for subcutaneous injections. The main patagia of the wing are the propatagium (also called the wing web) between the shoulder and carpus and the metapatagium between the thorax and wing.

Brood patch

This is a patch on the midventral chest between the caudal sternum and pubic bones. During the breeding season this patch loses feathers under the influence of estrogen and becomes thickened and vascular to provide extra warmth during egg incubation. In some species like gulls the number of brood patches is matched to the number of eggs in the clutch.

FEATHERS

Feathers are keratinized epidermis, which are derived from specialized follicles in the dermis. During growth there is a healthy arterial and venous blood supply to the follicle, which degenerates when the feather matures. Immature feathers will thus bleed if broken and are called “blood feathers” (Bauck, Orosz & Dorrestein 1997).

The feathering or plumage of birds can weigh 2 to 3 times than that of their bones. They are not attached to the skin evenly but are set in feather tracts called *pterylae* (Bauck, Orosz & Dorrestein 1997; Spearman 1971). Apteria (featherless regions) are also present and may be used for wing and leg movements and to provide space for these appendages to be tucked in. As they are not present in penguins they are also assumed to be an outlet for heat loss. The size and number of feathers is related to the metabolic rate, temperature, and body mass of each bird.

Role of feathers

Feathers play a vital role in protecting, insulating, and waterproofing the bird. They are also essential for flight and, often, courtship (Evans 1996).

Feather structure

The classic feather is the contour feather, which has a hollow shaft and feather vane. The main shaft is the *rachis* and the base is the *calumus*. The feather vane consists of a sheet of stiff filaments called barbs which extend at a 45 degree angle on either side from the rachis. Barbs have even finer filaments called barbules and these contain minute hooks that zip the feathers together, creating a smooth appearance (Evans 1996) (Fig. 6.77). Ostriches have feathers with barbules but they do not interlock, thus creating the fluffy appearance so beloved in the past as plumes for hats. Birds maintain this smooth appearance by preening, but if there is any lasting damage it can only be remedied when the feather is molted.

The rachis is grooved underneath and ends in a depression called the distal umbilicus. In some feathers a small down feather may emerge from this creating a fluffy appearance. The calamus or quill ends in the proximal umbilicus, which lies embedded in the feather follicle (Fig. 6.76).

Feather follicle

This is a tubular invagination of the epidermis with a dermal papilla at its base that projects up into the proximal umbilicus and has a rich supply of blood vessels (Fig. 6.78). After a feather becomes fully grown, germinal activity ceases at

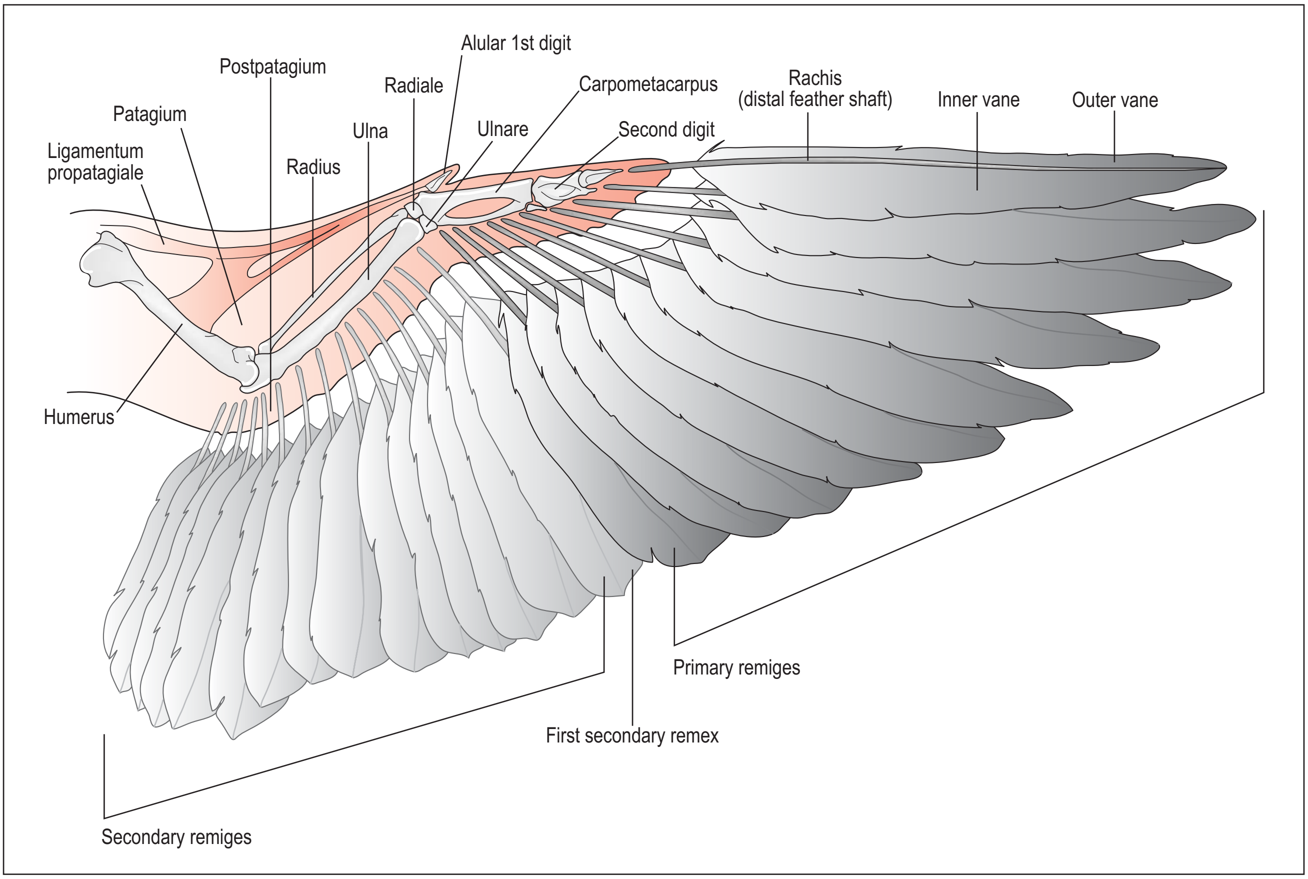

Alular 1st digit
Postpatagium
Radiale
Carpometacarpus
Rachis
(distal feather shaft)
Inner vane
Outer vane
Patagium
Ulna
Ulnare
Second digit
Ligamentum
propatagiale
Radius
Humerus
Primary remiges
First secondary remex
Secondary remiges

Figure 6.74 • Ventral view of wing showing insertion of primary and secondary contour feathers.

the base of the follicle and it enters a resting stage until the next molt. This feather papilla will continue to produce feathers throughout the bird's life (Evans 1996; Spearman 1971).

Adjacent feather follicles are linked by a network of smooth muscles lying in the dermis and each muscle is attached to the follicle by an elastic tendon. These muscles can act as a unit to raise or lower feathers, draw them apart or together. This can be used for sexual display or to fluff out feathers when cold to conserve heat. This is controlled by mechanoreceptors, the Herbst corpuscles, that lie adjacent to feather tracts. These are very sensitive to vibration and help to position the feathers.

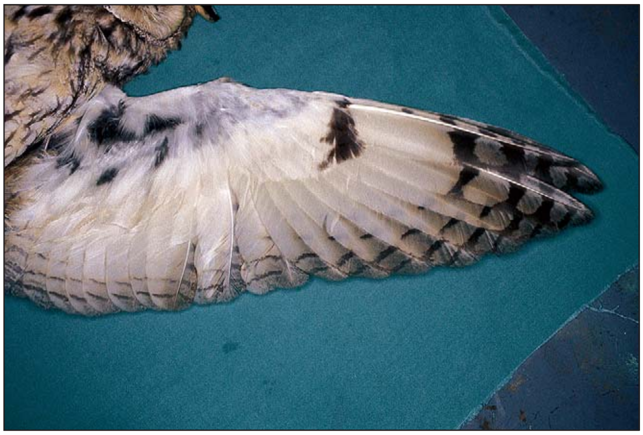


Figure 6.75 • Ventral view of wing of long eared owl (*Asio otus*).

Feather types

Contour feathers

These are the largest feathers and form the external appearance of adult birds. They are found on wings, tail, and body surface and are the feathers of flight. The wing feathers are called *remiges* (Latin for "rowers") while tail feathers are called *rectrices* (Latin for "rudder"). The number of each will vary; for example, budgies have 10 primaries and 11 secondaries on each wing and 6 pairs of rectrices (Evans 1996). Covert feathers are smaller feathers which cover the remiges and rectrices dorsally and ventrally. As they are purely for covering the body and play no role in flight, they are symmetrical. Ear coverts cover the external ear orifice and may help with hearing.

Flight feathers

Wing feathers

The wing feathers or remiges are made up of approximately 10 primaries and 10 to 20 secondaries, depending on the species (Figs. 6.74 and 6.75). The primaries are strongly

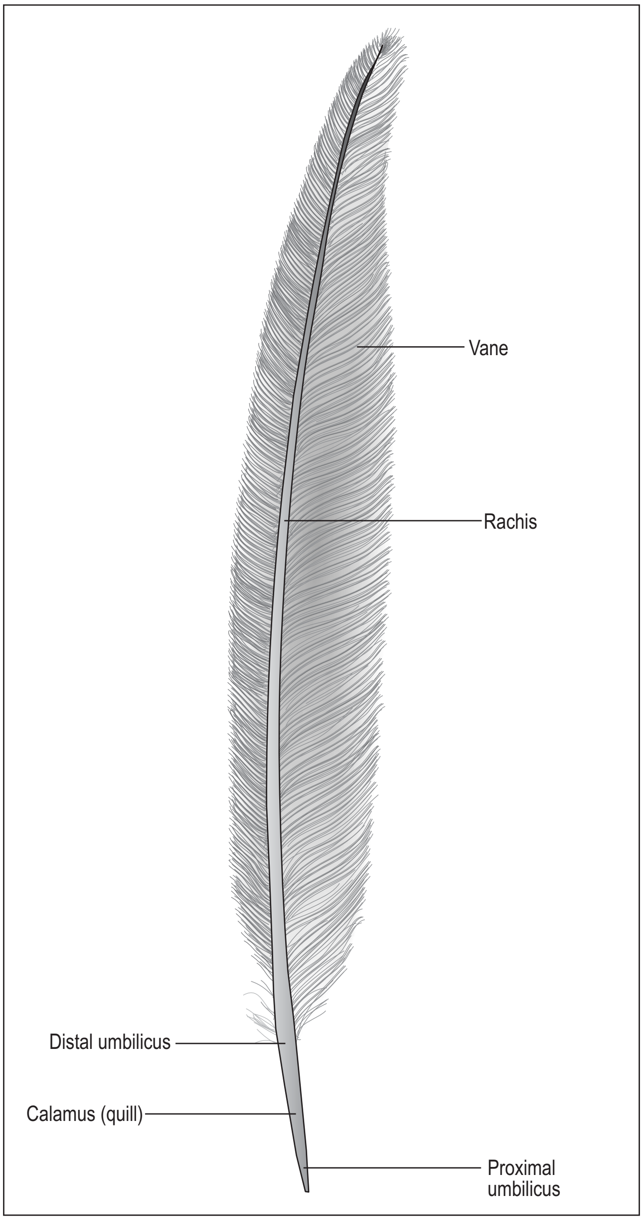

Vane
Rachis
Distal umbilicus
Calamus (quill)
Proximal umbilicus

Figure 6.76 • Contour wing feather (rectrix) showing asymmetry of vane.

attached dorsally from the carpus to the phalanges and are not very movable. Each one is asymmetric to act like its own individual airfoil. The secondaries are attached along the posterior edge of ulna and form the trailing edge of the wing. These are particularly enlarged in surface area in birds that soar. The secondaries have more mobility and are covered by the wing coverts.

The vanes of the wing feathers are asymmetrical, with the external side of the vane being narrower than the internal for aerodynamic flight. In many birds the distal end is narrowed so that when the wings are spread there is no overlapping but there are slots between each feather tip. This reduces the drag effect and allows each feather to act like a propeller blade (Spearman & Hardy 1985).

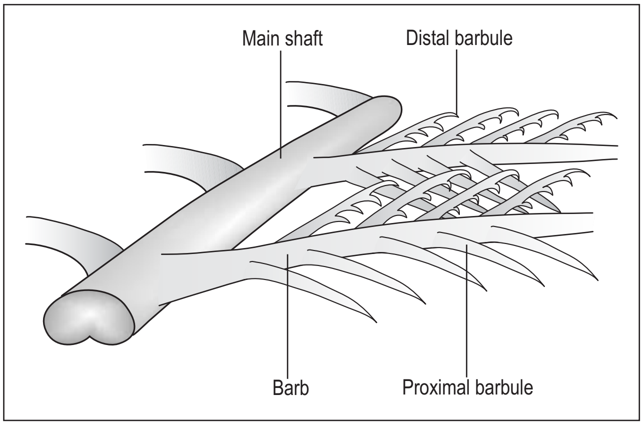

Main shaft
Distal barbule
Barb
Proximal barbule

Figure 6.77 • Detail of barbs, barbules and interlocking hooklets.

CLINICAL NOTE

The main difference between a feather and a mammalian hair is that the feather follicle contains a vascular core of dermis as well as epidermis (Fig. 6.78). This is why a feather may bleed profusely when plucked out and why blood feathers should not be cut when wing clipping (Bauck, Orosz & Dorrestein 1997).

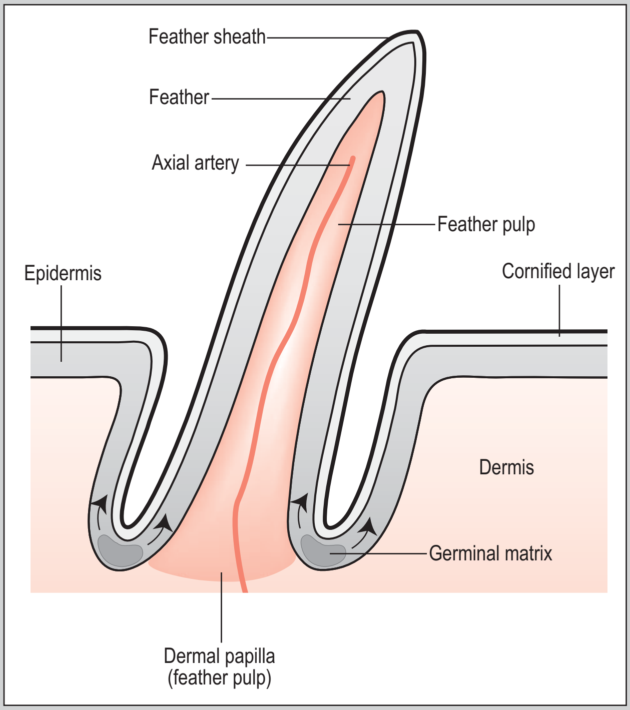

Feather sheath
Feather
Axial artery
Feather pulp
Epidermis
Cornified layer
Dermis
Germinal matrix
Dermal papilla (feather pulp)

Figure 6.78 • Development of a feather.
The axial core of dermis forms the pulp with a covering of epidermis. Unlike mammalian skin the dermis of developing feathers provides a rich blood supply – hence the term blood feather.

Tail feathers

The rectrices attach to the pygostyle and are used for steering and braking during flight. There are usually 6 pairs but numbers can vary from 4 to 10 pairs depending on species (Evans 1996).

Semiplumes

These appear fluffy, with a very long rachis that is longer than the barbs (Fig. 6.79a). As there are no barbules there is no smooth effect. These can often be found alongside feather margins, are good insulators and are often used for courtship.

Filoplumes

These are the avian equivalent of mammalian whiskers and act like sensory organs. They are bristle-like, with a long calumus and a fine tuft of barbs at the tip, and are often found in association with the follicles of contour feathers (Fig. 6.79c). These have nerve endings near their follicles which may help with aerodynamic adjustments of the contour feathers. They are absent in flightless birds like penguins and ostriches (Bauck, Orosz & Dorrestein 1997).

Down feathers

These are the converse of semi plumes with a small rachis (shorter than the barbs) and non-interlocking barbules, which makes them fluffy (Fig. 6.79b). They lie next to the body under the contour feathers in adults and are what gives chicks their fluffy appearance. The loose barbules trap air next to the skin and so these are the best feathers for providing thermal insulation.

GENERAL INTEREST

In sea ducks, like the Common Eider (*Somateria mollissima*) down feathers form an impervious layer of very dense feathers, which covers the whole thorax and abdomen. These insulating feathers are plucked during the breeding season to make a cosy nest for their young on rocky sea cliffs. In the past this down was much sought after for making quilts – hence the name “eiderdown” (Spearman & Hardy 1985).

Powder down

These are specialized down feathers which produce a fine powder keratin dust from the barbs. This talc-like powder is then coated over the plumage during preening. It is found in many parrots, like cockatoos and African grays, and its absence can often be the first sign of the circovirus causing Psittacine Beak and Feather Disease. In pigeons the production of powder down has been associated in humans with allergic alveolitis or “pigeon fanciers lung” (Spearman & Hardy 1985).

Hyopenna

These are called afterfeathers and protrude from the base of the rachis of contour feathers. They have a stiff rachis and almost no barbules (Fig. 6.79e).

Bristles

These have a stiff rachis and a few barbs at the proximal end (Fig. 6.79d). These are found at the base of the eyelids, nares, and mouth. They have both sensory and protective functions similar to mammalian whiskers.

Feather color

The wonderful range of avian feather color plays a major role in camouflage, courtship, and protection from heat and light. The color can be produced by pigments like melanin, carotenoids and porphyrins or the structural effects of white light on the feathers.

Melanin is what gives blackbirds and crows their black appearance and also produces gray and brown. It is the most common pigment found in birds and is synthesized from the amino acid tyrosine. Feathers containing melanin are stronger as they usually have increased amounts of keratin (Spearman 1971; Spearman & Hardy 1985; Welty 1982a).

CLINICAL NOTE

As feathers containing melanin pigment are stronger, many white birds like gulls often have blackened tips on the primary feathers to protect against wear and tear.

Carotenoids cannot be synthesized but are obtained by birds from plants in their diet. They are red, orange, and yellow pigments and are responsible for the canary yellow, cardinal red, and flamingo pink coloration. They rarely affect flight feathers but mainly affect other contour feathers, especially of the breast and back (Spearman 1971; Spearman & Hardy 1985; Welty 1982a).

GENERAL INTEREST

Flamingos are able to oxidize yellow or beta-carotene to red ketocarotenoids. Newly hatched chicks have no pigmentation but receive it from their parents in the crop milk. These yellow pigments come from plant foods in the Andean flamingo (*Phoenicopterus andinus*) or from algae, crustaceans, and molluscs in other flamingo species.

Porphyrins are nitrogenous pigments synthesized by birds and form green, red and some browns. They are found in owls, pigeons, and gallinaceous birds. These colors fluoresce when exposed to ultraviolet light.

Structural colors

Birds do not have a true blue pigment (Spearman & Hardy 1985). Instead, when white light is scattered by the feathers the short wavelength red end of the spectrum is absorbed while the blue end is reflected. This effect, known as Tyndall scattering, is what makes the sky blue. Although some green is produced by porphyrin pigments it is more commonly produced by a combination of yellow carotenoids and the Tyndall effect (Spearman 1971; Spearman & Hardy 1985; Welty 1982a).

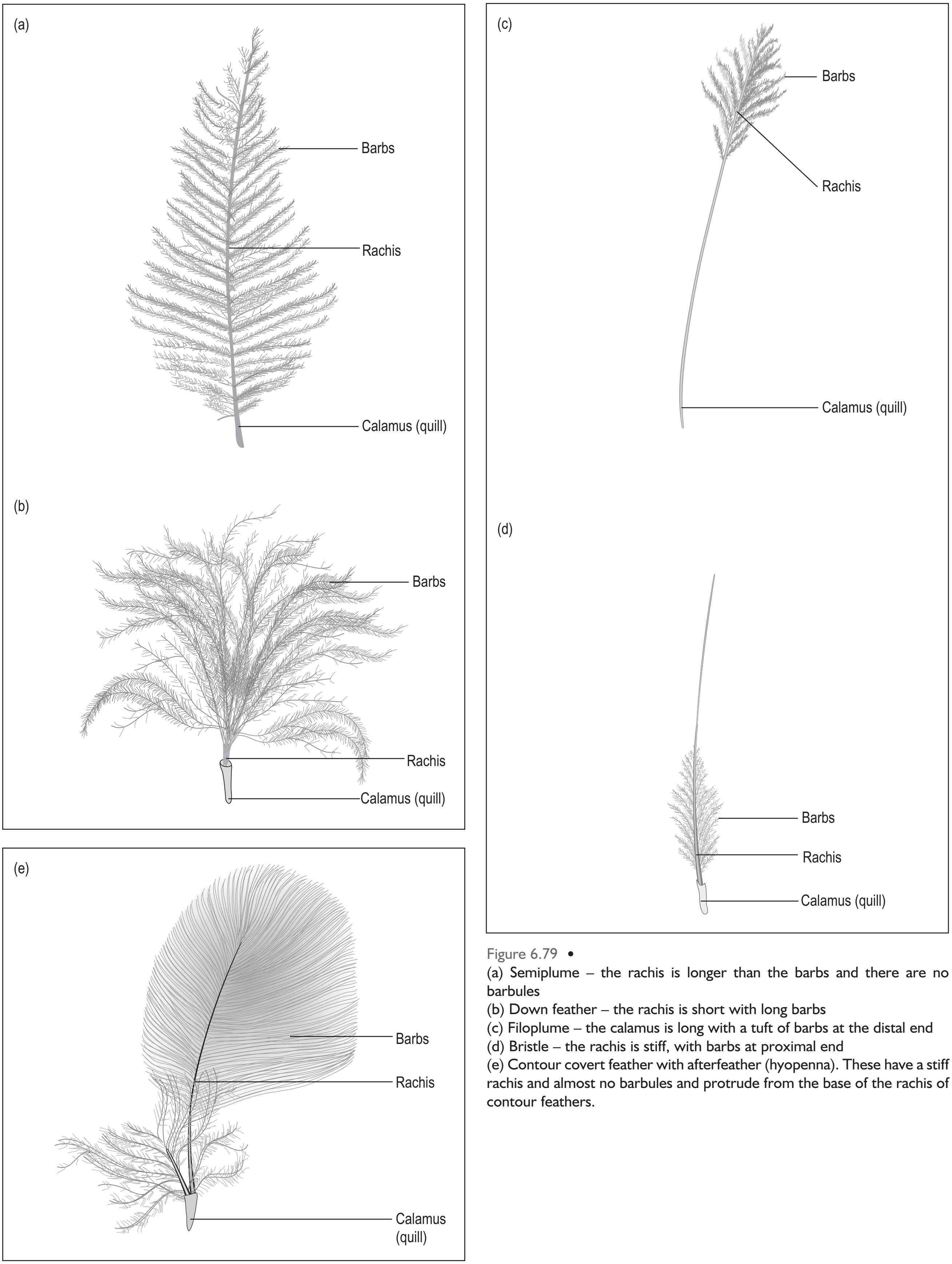
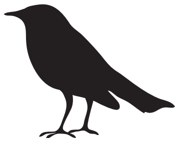
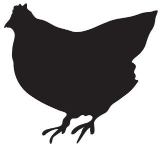
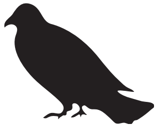

(a)
Barbs
Rachis
Calamus (quill)
(b)
Barbs
Rachis
Calamus (quill)
(c)
Barbs
Rachis
Calamus (quill)
(d)
Barbs
Rachis
Calamus (quill)
(e)
Barbs
Rachis
Calamus (quill)

Figure 6.79 •
(a) Semiplume – the rachis is longer than the barbs and there are no barbules
(b) Down feather – the rachis is short with long barbs
(c) Filoplume – the calamus is long with a tuft of barbs at the distal end
(d) Bristle – the rachis is stiff, with barbs at proximal end
(e) Contour covert feather with afterfeather (hyopenna). These have a stiff rachis and almost no barbules and protrude from the base of the rachis of contour feathers.

Table 6.6 Anatomical and physiological characteristics of the more common avian orders

	Psittaciformes[1,2]	 **Passeriformes**[3-5]	**Falconiformes**[6]	 **Galliformes**[7,8]	 **Columbiformes**[9-13]	**Anseriformes**[14-16]
Longevity	50–80 yrs (Macaws)	5 yrs (Zebra Finch) - 44 yrs+ (Raven)	10–20 yrs	Turkeys, Domestic Fowl - up to 10 yrs	20–30 yrs	10 (Ducks) - 25 yrs (Swans/geese)
Weight range	50 g (Budgie) - 1–1.5 kg (Scarlet Macaw)	10 g (Zebra finch) - 1.5 kg (Raven)	120 g (Kestrel) - 14 kg (Condor)	1.2 kg (Guinea fowl) - 2.2 kg (Domestic fowl)	Domestic pigeon 350–500 g (from 50 g–1200 g)	300 g (Pygmy goose) - 13.6 kg (Trumpeter swan)
Skeleton						
Type of Foot	Zygodactyl Vestigial clavicles	Anisodactyl Extra muscle for perching	Anisodactyl (osprey - semi-zygodactyl) Carpal ossicle within Lig. Propatagiale Ossified flexor tendons in some species Fused notarium	Anisodactyl Spurs often present V shaped furcula Notched sternum Heavily muscled legs Fused notarium	Anisodactyl Fused notarium	Anisodactyl/palmate Sigmoid neck Short femurs & metatarsus Long tibiotarsus Separate thoracic vertebrae
Cardiovascular						
		Highest BMR and temperature of all Largest heart for size		Well defined sinus venosus Turkey has highest BP of all	Vascular plexus on neck (*plexus venosus intracutaneus collaris*)	Lymph nodes Heat loss through legs and webbed feet
Respiratory						
Syrinx	Simple syrinx	Well-developed complex syrinx	Poorly developed syrinx	Simple syrinx		Syringeal bulla in male ducks
Sinuses	Right/left nasal sinus communication	No communication right/left sinus				Salt glands present
Airsacs	Well-developed infraorbital sinus	7 airsacs (Cranial thoracics fused with clavicular)		9 airsacs (except turkey with 7)		Long trachea coiled in sternum (Trumpeter swan)
Digestion						
Type of Diet	Omnivorous, granivorous	Omnivorous, insectivorous, granivorous	Carnivorous (piscivorous)	Omnivorous (granivorous)	Mainly granivores (some frugivores)	Mainly herbivorous (some omnivorous)
Cere	Cere present, often feathered	Cere absent	Cere present	Cere present	Cere usually snow white	Often fleshy cere

Continued

Table 6.6 Anatomical and physiological characteristics of the more common avian orders—cont'd

	Psittaciformes^{1,2}	**Passeriformes**$^{3\text{-}5}$	**Falconiformes**^{6}	**Galliformes**^{7,8}	**Columbiformes**$^{9\text{-}13}$	**Anseriformes**$^{14\text{-}16}$
Tongue	Intrinsic muscular tongue	Narrow triangular tongue	Simple tongue	Simple triangular tongue	Drink by sucking with tongue	Tongue has bristles
Beak	Prokinetic beak	Prokinetic beak	Hooked beak	Prokinetic beak	Rhynchokinetic beak	Rhynchokinetic beak with lamellae
	Craniofacial hinge	Ridged hard palate (seed eaters)	Talons used for feeding			Beak tip organ
Crop/caecae	Crop present, caecae absent	Crop present, rudimentary caecae	Fusiform crop, small caecae	Large crop, well-developed caecae	Bilobed crop – crop milk, small caecae	Simple fusiform crop, large cecae
Gall bladder	Gall bladder often absent	Gall bladder absent	Small gizzard, no grit	Large gizzard, gall bladder present	Large gizzard with grit, gall bladder absent	Large gizzard with grit, gall bladder present
Spleen	Spherical spleen	Oblong spleen	Egestion of pellets	Oval spleen	Oval spleen	Spleen triangular
Reproduction						
Sexual maturity	6 mth–1 yr (Small), 3–6 yrs (large)	9 mths –1 yr (songbirds)	1–3 yrs (varies with species)	4.5–7 months (Domestic fowl)	5–12 months	Ducks 1yr, geese 2 yrs, swans 5yrs
Phallus	No phallus	No phallus	No phallus	Non-protrusible phallus	No phallus	Protrusible phallus
Sexing	Many sexually monomorphic	Often sexual dimorphism	Sexual dimorphism present	Sexual dimorphism	Sexually monomorphic	Sexual dimorphism only in ducks
		Seminal glottus in male	Female 30% bigger	Brood patch	Monagamous	Swans and geese monagamous
Young	Altricial young	Altricial young	Altricial young	Nidifugous young	Altricial young	Nidifugous young
		Dramatic enlargement breeding gonads	2 ovaries occasionally found	Epididymal appendix attached to adrenals	Usually two eggs	Easily imprinted
						Left oviduct membrane in juveniles
Integument						
Powder down	Powder down feathers			Spurs, wattles and combs	Powder down produced	Dense down/waterproof plumage
	Some lack uropygial gland				No uropygial glands	Highly developed uropygial gland
Feathers	10 primaries, 6 pairs rectrices					Flightless molt in some species
Special Sense						
Eyeball shape	Flat	Globular	Globose	Flat	Flat	Flat
	Poorly developed scleral ossicles		15 scleral ossicles	14–15 scleral ossicles		Poorly developed eye ossicles
	Complete orbit	Corvids have large optic nerve	Large eyes and optic nerve			
	Beak tip organ present on mandible		High visual acuity - two foveae		Ability to hear infrasound	

Superscript numbers in this table represent references, listed below. For full reference please see reference list
1-Evans 1996; 2-King & McLellan 1984; 3-Dorrestein 1997b; 4-Jones & Slater 1999; 5-King & McLelland 1984; 6-King & McLelland 1984; 7-Gerlach 1997a; 8-King & McLellan 1984; 9-Harlin 1994; 10-Harper 1996; 11-Hooimeijer & Dorrestein 1997; 12-Hutchinson 1999; 13-King & McLellan 1984; 14-Fowler 1986; 15-Gerlack 1997b; 16-King & McLelland 1984

Iridescence (like the rainbow coloring of an oil slick), as seen in starlings and peacocks, is a combination of melanin pigment with structural breakdown of light through the feather barbules. This effect means the color will change with the angle from which it is viewed (Welty 1982a).

Molting

This is the replacement of feathers and is a continuous process to avoid the bird becoming bald and flightless. Molting occurs because the emerging feather ejects the old feather from its follicle causing it to be shed (Spearman & Hardy 1985). Before the barbs are released they are encased in a feather sheath called a *pinfeather*. Birds usually molt the inside primaries first and then stagger the loss of the rest of the wing feathers(Spearman 1971).

Feathers are held in place in follicles by the action of the follicular muscle under the control of the autonomic nervous system. When a bird is frightened this may relax, causing the bird to shed feathers in what is called a "fright molt" (Bauck, Orosz & Dorrestein 1997). Cut feathers or plucked feathers do not regrow until the feather shaft is lost in the molt and the new one grows from the feather papilla.

Triggers for molting

Factors influencing molting are nutrition, reproduction, time of year, temperature, and light. It also depends on habitat and whether the bird is migratory or not. Young birds molt their juvenile feathers before they become adults and often go through a series of subadult plumages. Adult birds usually molt after breeding (post nuptial or winter plumage) when the levels of estrogen and androgens drop. Some birds keep the new set for the next 12 months while some change to a brighter nuptial or breeding plumage for courtship display in the mating season (Bauck, Orosz & Dorrestein 1997). Ducks and geese lose all their contour feathers at once and this renders them temporarily flightless.

Molting is a time of intense stress on a bird with increased demands for protein (especially amino acids lysine, cystine, and arginine), calcium, and iron. Therefore birds that lose feathers due to illness or self-mutilation have high demands for good nutrition. Heat loss is increased due to feather loss so energy intake must be increased to sustain the increased metabolic rate. In fact, the total draw of energy and protein reserves during molting can cause the metabolic rate to increase by 15 to 25%.

Control of molting

Photoperiod detected via the hypthalamus and anterior pituitary triggers the release of the thyroid and gonadal hormones. Thryoxine stimulates the feather follicles and growth of the plumage while androgen and estrogen appear to inhibit molt until after the breeding season. Progesterone prevents ovulation and induces molt by stimulating the feather papillae. Dietary deficiencies, especially low protein diets, will also inhibit molting (Spearman 1971).

KEY POINTS

- Avian skin is thin and inelastic with a bacteriostatic lipid layer.
- The patagia (skin webs) are useful sites for subcutaneous injections.
- Damaged feathers can only be replaced at the next molt.
- Good levels of nutrition are essential to aid molting and produce new healthy feathers. Extra protein, calcium and iron is important.
- Newly emerging feathers, called blood or pin feathers, are highly vascular so beware cutting these if wing clipping.

REFERENCES

Akester, A. R. (1971) The blood vascular system. In D. J. Bell & B. M. Freeman (eds.), *Physiology and biochemistry of the domestic fowl*. Vol. 2. London: Academic Press. pp. 783–837.

Akester, A. R. (1984) The cardiovascular system. In B. M. Freeman (ed.), *Physiology and biochemistry of the domestic fowl*. Vol. 5. London: Academic Press. pp. 172–257.

Archer, R. K. (1971) Blood coagulation. In D. J. Bell & B. M. Freeman (eds.), *Physiology and biochemistry of the domestic fowl*. Vol. 2. London: Academic Press. pp. 897–910.

Bauck, L., Orosz, S., & Dorrestein, G. M. (1997) Avian dermatology. In R. B. Altman, S. L. Clubb, G. M. Dorrestein & K. Quesenberry (eds.), *Avian medicine and surgery*. Philadelphia: WB Saunders. pp. 540–562.

Bezuidenhout, A. J. (1999) Anatomy. In D. C. Deeming (ed.), *The ostrich, biology, production and health*. Oxford: CABI Publishing. pp. 13–51.

Blem, C. R. (2000) Energy balance. In G. C. Whittow (ed.), *Sturkie's avian physiology*, 5th edn. San Diego, Calif.: Academic Press. pp. 327–339.

Brackenbury, J. H. (1987) Ventilation of the lung-air sac system. In T. J. Sellar (ed.), *Bird respiration*. Vol. 1. Boca Raton, Fla.: CRC Press. pp. 39–71.

Brown, R. E., & Klemm, R. D. (1990) Surgical anatomy of the propatagium. In *The proceedings of the Association of Avian Veterinarians annual conference*. Lake Worth, Fla.: AAV.

Butler, P. J., & Bishop, C. M. (2000) Flight. In G. C. Whittow (ed.), *Sturkie's avian physiology*, 5th edn. San Diego, Calif.: Academic Press. pp. 391–428.

Dawson, W. R., & Whittow, G. C. (2000) Regulation of body temperature. In G. C. Whittow (ed.), *Sturkie's avian physiology*, 5th edn. San Diego, Calif.: Academic Press. pp. 344–379.

Denbow, D. M. (2000) Gastrointestinal anatomy and physiology. In G. C. Whittow (ed.), *Sturkie's avian physiology*, 5th edn. San Diego, Calif.: Academic Press. pp. 299–321.

Dorrestein, G. M. (1997a) Metabolism, pharmacology and therapy. In R. B. Altman, S. L. Clubb, G. M. Dorrestein & K. Quesenberry (eds.), *Avian medicine and surgery*. Philadelphia: WB Saunders. pp. 661–670.

Dorrestein, G. M. (1997b) Passerines. In R. B. Altman, S. L. Clubb, G. M. Dorrestein & K. Quesenberry (eds.), *Avian medicine and surgery*. Philadelphia: WB Saunders. pp. 867–886.

Duke, G. E. (1986) Alimentary canal: Secretion and digestion, special digestive functions, and absorption. In P. D. Sturkie (ed.), *Avian physiology*. New York: Springer. pp. 289–302.

Duke, G. E. (1993) Avian digestion. In M. J. Swenson & W. O. Reece (eds.), *Dukes physiology of domestic animals*, 11th edn. Ithaca, N.Y.: Cornell University Press. pp. 428–437.

Duncker, H. R. (1979) Coelomic cavities. In A. S. King & J. McLelland (eds.), *Form and function in birds*. Vol. 1. London: Academic Press. pp. 39–69.

Dyce, K. M., Sack, W. O., & Wensing, C. J. (2002) Avian anatomy. In K. M. Dyce, W. O. Sack. & C. J. Wensing (eds.), *Textbook of veterinary anatomy*, 3rd edn. Philadelphia: WB Saunders. pp. 799–825.

Echols, S. (1999) Collecting diagnostic samples in avian patients. In D. R. Reavill (ed.), *Clinical pathology and sample collection*. The Veterinary Clinics of North America, Exotic Animal Practice, Vol 2. Philadelphia: WB Saunders. pp. 621–649.

Evans, H. E. (1996) Anatomy of the budgie and other birds. In W. Rosskopf & R. Woerpel (eds.), *Diseases of cage and aviary birds*, 3rd edn. Baltimore: Williams & Wilkins. pp. 79–163.

Fedde, M. R. (1993) Respiration in birds. In M. J. Swenson & W. O. Reece (eds.), *Dukes physiology of domestic animals*, 11th edn. Ithaca, N.Y.: Cornell University Press. pp. 294–303.

Fowler, M. E. (ed.) (1986) *Zoo and wildlife medicine*, 2nd edn. Philadelphia: WB Saunders. Ducks, geese, swans and screamers (Anseriformes).

Freeman, B.M. (1971) The corpuscles and the physical characteristics of blood. In D. J. Bell & B. M. Freeman (eds.), *Physiology and biochemistry of the domestic fowl*. Vol. 2. London: Academic Press. pp. 841–852.

Gaunt, A. S. (1987) Phonation. In T. J. Sellar (ed.), *Bird respiration*, Vol 1. Boca Raton, Fla.: CRC Press. pp. 71–97.

Gerlach, H. (1997a) Galliformes. In R. B. Altman, S. L. Clubb, G. M. Dorrestein & K. Quesenberry (eds.), *Avian medicine and surgery*. Philadelphia: WB Saunders. pp. 944–959.

Gerlach, H. (1997b) Anatiformes. In R. B. Altman, S. L. Clubb, G. M. Dorrestein & K. Quesenberry (eds.), *Avian Medicine and Surgery*. Philadelphia: WB Saunders. pp. 960–972.

Gilbert, A. G. (1979) Female genital organs. In A. S. King & J. McLelland (eds.), *Form and function in birds*. Vol. 1. London: Academic Press. pp. 237–361.

Goldstein, D. L., & Skadhauge, E. (2000) Renal and extrarenal regulation of body fluid composition. In G. C. Whittow (ed.), *Sturkie's avian physiology*, 5th edn. San Diego, Calif.: Academic Press. pp. 265–291.

Gunturkun, O. (2000) Sensory physiology: Vision. In G. C. Whittow (ed.), *Sturkie's avian physiology*, 5th edn. San Diego, Calif.: Academic Press. pp. 1–14.

Harcourt-Brown, N. H. (1996) Pelvic limb problems. In P. H. Benyon (ed.), *BSAVA Manual of psittacine birds*. Gloucester, UK: BSAVA. pp. 123–133.

Harlin, R. W. (1994) Pigeons. In K. E. Quesenberry & E.V. Hillyer (eds), *Exotic Pet Medicine.* Vol. 2. The Veterinary Clinics of North America Small Animal Practice *24*(1), 157–173.

Harper, F. D. (1996) Pigeons – husbandry and nutrition. In P. H. Benyon (ed.), *BSAVA Manual of raptors, pigeons and waterfowl*. Gloucester, UK: BSAVA. pp. 233–238.

Hazelwood, R. L. (2000) Pancreas. In G. C. Whittow (ed.), *Sturkie's avian physiology*, 5th edn. San Diego, Calif.: Academic Press. pp. 539–555.

Hill, K. J. (1971a) The structure of the alimentary tract. In D. J. Bell & B. M. Freeman (eds.), *Physiology and biochemistry of the domestic fowl*. Vol. 1. London: Academic Press. pp. 1–22.

Hill, K. J. (1971b) The physiology of digestion. In D. J. Bell & B. M. Freeman (eds.), *Physiology and biochemistry of the domestic fowl*. Vol. 1. London: Academic Press. pp. 25–47.

Hinds, D. S., & Calder, W. A. (1971) Tracheal dead space in the respiration of birds. *Evolution 25*, 429–440.

Hodges, R. D. (1981) Endocrine glands. In A. S. King & J. McLelland (eds.), *Form and function in birds*. Vol. 2. London: Academic Press. pp. 149–235.

Hodges, R. D. (1979) The blood cells. In A. S. King & J. McLelland (eds.), *Form and function in birds*. Vol. 1. London: Academic Press. pp. 361–379.

Hoefer, H. L., Orosz, S., & Dorrestein, G. M. (1997) The gastrointestinal tract. In R. B. Altman, S. L. Clubb, G. M. Dorrestein & K. Quesenberry (eds.), *Avian medicine and surgery*. Philadelphia: WB Saunders. pp. 412–419.

Hooimeijer, J., & Dorrestein, G. M. (1997) Pigeons and doves. In R. B. Altman, S. L. Clubb, G. M. Dorrestein & K. Quesenberry (eds.), *Avian medicine and surgery*. Philadelphia: WB Saunders. pp. 886–910.

Hutchinson, R. E. (1999) Doves and pigeons. In T. Poole (ed.), *The UFAW handbook: The care and management of laboratory animals*, 7th edn. Vol. 1. Oxford: Blackwell Science. pp. 714–721.

Johnson, A. L. (2000) Reproduction in the female. In G. C. Whittow (ed.), *Sturkie's avian physiology*, 5th edn. San Diego, Calif.: Academic Press. pp. 569–596.

Johnson, O. W. (1979) Urinary organs. In A. S. King & J. McLelland (eds.), *Form and function in birds*. Vol. 1. London: Academic Press. pp. 183–237.

Jones, A. E., & Slater, P. J. (1999) The zebra finch. In T. Poole (ed.), *The UFAW handbook: The care and management of laboratory animals*, 7th edn. Vol. 1. Oxford: Blackwell Science. pp. 722–731.

Jukes, M. G. (1971) Control of respiration. In D. J. Bell & B. M. Freeman (eds.), *Physiology and biochemistry of the domestic fowl*. Vol. 1. London: Academic Press. pp. 172–185.

Kern, T. J. (1997) Disorders of the special senses. In R. B. Altman, S. L. Clubb, G. M. Dorrestein & K. Quesenberry (eds.), *Avian medicine and surgery*. Philadelphia: WB Saunders. pp. 563–566.

King, A. S. (1981a) Cloaca. In A. S. King & J. McLelland (eds.), *Form and function in birds*. Vol. 2. London: Academic Press. pp. 63–107.

King, A. S. (1981b) Phallus. In A. S. King & J. McLelland (eds.), *Form and function in birds*. Vol. 2. London: Academic Press. pp. 107–149.

King, A. S. (1989) Functional anatomy of the syrinx. In A. S. King & J. McLelland (eds.), *Form and function in birds*. Vol. 4. London: Academic Press. pp. 105–192.

King, A. S., & King, D. Z. (1979) Avian morphology. In A. S. King & J. McLelland (eds.), *Form and function in birds*. Vol. 1. London: Academic Press. pp. 1–38.

King, A. S., & McLelland, J. (eds.) (1975) *Outlines of avian anatomy*. London: Bailliere Tindall. The coelomic cavities; pp. 30–33.

King, A. S., & McLelland, J. (1984) *Birds – Their structure and function*, 2nd edn. London: Bailliere Tindall.

King, A. S., & Molony, V. (1971) The anatomy of respiration. In D. J. Bell & B. M. Freeman (eds.), *Physiology and biochemistry of the domestic fowl*. Vol. 1. London: Academic Press. pp. 93–169.

King, A. S., & Payne, D. C. (1964) Normal breathing and the effects of posture in *Gallus Domesticus*. *Journal of Physiology (Lond) 174*, 340–347.

King, G., & Custance, D. R. (1982) *Colour atlas of vertebrate anatomy*. Oxford: Blackwell science publications. The pigeon; pp. 5.1–6.1.

King-Smith, P. E. (1971) Special senses. In D. J. Bell & B. M. Freeman (eds.), *Physiology and biochemistry of the domestic fowl*. Vol. 2. London: Academic Press. pp. 1039–1080.

Kirby, J. D., & Froman, D. P. (2000) Reproduction in the male. In G. C. Whittow (ed.), *Sturkie's Avian Physiology*, 5th edn. San Diego, Calif.: Academic Press. pp. 597–612.

Kirkwood, J. K. (1999) Introduction to birds. In T. Poole (ed.), *The UFAW handbook: The care and management of laboratory animals*, 7th edn. Vol. 1. Oxford: Blackwell Science. pp. 661–670.

Klasing, K. C. (1998) Anatomy and physiology of the digestive system. In K.C. Klasing (ed.), *Comparative avian nutrition*. Oxford: CABI Publishing. pp. 9–36.

Koch, T. (1973) Locomotion system. In B. H. Skold & L. Devries (eds.), *Anatomy of the chicken and domestic birds*. Ames: Iowa State University Press. pp. 6–65.

Lake, P. E. (1981) Male genital Organs. In A. S. King & J. McLelland (eds.), *Form and function in birds*. Vol. 2. London: Academic Press. pp. 1–63.

Lasiewski, R. C. (1972) Respiratory function of birds. In D. S. Farner & J. R. King (eds.), *Avian Biology*. Vol. 2. New York: Academic Press. pp. 288–335.

Maina, J. N. (1989) The morphometry of the avian lung. In A. S. King & J. McLelland (eds.), *Form and function in birds*. Vol. 4. London: Academic Press. pp. 307–368.

Maina, J. N. (1996) Perspectives on the structure and function of birds. In W. Rosskopf & R. Woerpel (eds.), *Diseases of cage and aviary birds*, 3rd edn. Baltimore: William & Wilkins. pp. 163–217.

Martin, G. R. (1985) Eye. In A. S. King & J. McLelland (eds.), *Form and function in birds*. Vol. 3. London: Academic Press. pp. 311–375.

Mason, J. R., & Clark, L. (2000) The chemical senses in birds. In G. C. Whittow (ed.), *Sturkie's avian physiology*, 5th edn. San Diego, Calif.: Academic Press. pp. 39–51.

McLelland, J. (1979) Digestive system. In A. S. King & J. McLelland (eds.), *Form and function in birds*. Vol. 1. London: Academic Press. pp. 69–181.

McLelland, J. (1990) *A colour atlas of avian anatomy*. Aylesbury, UK: Wolfe.

McLelland, J., & Molony, V. (1983) Respiration. In B. M. Freeman (ed.), *Physiology and biochemistry of the domestic fowl*. Vol. 4. London: Academic Press. pp. 63–85.

Millam, J. R. (1997) Reproductive physiology. In R. B. Altman, S. L. Clubb, G. M. Dorrestein & K. Quesenberry (eds.), *Avian medicine and surgery*. Philadelphia: WB Saunders. pp. 12–27.

Necker, R. (2000) The avian ear and hearing. In G. C. Whittow (ed.), *Sturkie's avian physiology*, 5th edn. San Diego, Calif.: Academic Press. pp. 21–35.

Oglesbee, B. L., Orosz, S., & Dorrestein, G. M. (1997) The endocrine system. In R. B. Altman, S. L. Clubb, G. M. Dorrestein & K. Quesenberry (eds.), *Avian medicine and surgery*. Philadelphia: WB Saunders. pp. 475–488.

Orosz, S. E. (2002) Clinical considerations of the thoracic limb. In T. N. Tully (ed.), *The veterinary clinics of North America: Exotic animal practice*. Vol. 5, Orthopedics. Philadelphia: WB Saunders. pp. 31–48.

Orosz, S. E., Ensley, P. K., & Haynes, C. J. (1992) Avian surgical anatomy: Thoracic and pelvic limbs. Philadelphia: WB Saunders.

Orosz, S., Dorrestein, G. M., & Speer, B. L. (1997) Urogenital disorders. In R. B. Altman, S. L. Clubb, G. M. Dorrestein & K. Quesenberry (eds.), *Avian Medicine and Surgery*. Philadelphia: WB Saunders. pp. 614–644.

Payne, L. N. (1984) The lymphoid system. In B. M. Freeman (ed.), *Physiology and biochemistry of the domestic fowl*. Vol. 5. London: Academic Press. pp. 985–1031.

Phalen, D. N. (2000) Avian renal disorders. In A. M. Fudge (ed.), *Laboratory medicine – Avian and exotic pets*. pp. 61–68. Philadelphia: WB Saunders.

Powell, F. L. (2000) Respiration. In G. C. Whittow (ed.), *Sturkie's avian physiology*, 5th edn. San Diego, Calif.: Academic Press. pp. 233–259.

Powers, L. V. (2000) Avian haemostasis. In A. M. Fudge (ed.), *Laboratory medicine: Avian and exotic pets*. Philadelphia: WB Saunders. pp. 35–47.

Quesenberry, K., Orosz, S., & Dorrestein, G. M. (1997) Musculoskeletal system. In R. B. Altman, S. L. Clubb, G. M. Dorrestein & K. Quesenberry (eds.), *Avian medicine and surgery*. Philadelphia: WB Saunders. pp. 517–523.

Rae, M. (2000) Avian endocrine disorders. In A. M. Fudge (ed.), *Laboratory medicine: Avian and exotic pets*. Philadelphia: WB Saunders. pp. 76–89.

Raikow, R. J. (1985) Locomotor system. In A. S. King & J. McLelland (eds.), *Form and function in birds*. Vol. 3. London: Academic Press. pp. 57–149.

Rose, M. E. (1981) Lymphatic system. In A. S. King & J. McLelland (eds.), *Form and function in birds*. Vol. 2. London: Academic Press. pp. 341–385.

Rosenthal, K., Orosz, S, & Dorrestein, G. M. (1997a) The nervous system. In R. B. Altman, S. L. Clubb, G. M. Dorrestein & K. Quesenberry (eds.), *Avian medicine and surgery*. Philadelphia: WB Saunders. pp. 454–460.

Rosenthal, K., Miller, M., Orosz, S., & Dorrestein, G. M. (1997b) The cardiovascular system. In R. B. Altman, S. L. Clubb, G. M. Dorrestein & K. Quesenberry (eds.), *Avian medicine and surgery*. Philadelphia: WB Saunders. pp. 489–500.

Scheid, P., & Piiper, J. (1971) Direct measurement of the pathway of respired gas in duck lungs. *Respiration Physiology 11*, 308–314.

Scheid, P., & Piiper, J. (1972) Cross current gas exchange in avian lungs: Effect of reversed parabronchial air flow in ducks. *Respiration Physiology 16*, 304–312.

Scheid, P., & Piiper, J. (1987) Gas exchange and transport. In T. J. Sellar (ed.), *Bird respiration*, Vol. 1. Boca Raton, Fla.: CRC Press. pp. 97–131.

Schmidt, R. E. (1997) Immune system. In R. B. Altman, S. L. Clubb, G. M. Dorrestein & K. Quesenberry (eds.), *Avian medicine and surgery*. Philadelphia: WB Saunders. pp. 645–652.

Schmidt-Nielsen, K. (1975) Recent advances in avian respiration. In M. Peaker (ed.), *Symposia of the Zoological Society of London, No 35: Avian physiology*. London: Academic Press. pp. 33–47.

Schmidt-Nielson, K. (1990) *Animal physiology – adaptation and environment*, 4th edn. Cambridge, UK: Cambridge University Press. pp. 42–47.

Shoemaker, V. H. (1972) Osmoregulation and excretion in Birds. In D. S. Farner & J. R. King (eds.), *Avian Biology*. Vol. 2. New York: Academic Press. pp. 527–551.

Siller, W. G. (1971) Structure of the kidney. In D. J. Bell & B. M. Freeman (eds.), *Physiology and biochemistry of the domestic fowl*. Vol. 1. London: Academic Press. pp. 197–229.

Siller, W. G. (1983) Structure of the kidney. In B. M. Freeman (ed.), *Physiology and biochemistry of the domestic fowl*. Vol. 4. London: Academic Press. pp. 91–104.

Smith, B. J., & Smith, S. A. (1997) Radiology. In R. B. Altman, S. L. Clubb, G. M. Dorrestein & K. Quesenberry (eds.), *Avian medicine and surgery*. Philadelphia: WB Saunders. pp. 170–200.

Smith, F. M., West, N. H., & Jones, D. R. (2000) The cardiovascular system. In G. C. Whittow (ed.), *Sturkie's avian physiology*, 5th edn. San Diego, Calif.: Academic Press. pp. 141–223.

Spearman, R. I. (1983) Integumentary system. In B. M. Freeman (ed.), *Physiology and biochemistry of the domestic fowl*. Vol. 4. London: Academic Press. pp. 211–217.

Spearman, R. I. (1971) Integumentary system. In D. J. Bell & B. M. Freeman (eds.), *Physiology and biochemistry of the domestic fowl*. Vol. 2. London: Academic Press. pp. 603–619.

Spearman, R. I., & Hardy, J. A. (1985) Integument. In A. S. King & J. McLelland (eds.), *Form and function in birds*. Vol. 3. London: Academic Press. pp. 1–57.

Sykes, A. H. (1971) Formation and composition of urine. In D. J. Bell & B. M. Freeman (eds.), *Physiology and biochemistry of the domestic fowl*. Vol. 1. London: Academic Press. pp. 233–276.

Taylor, T. G., Simkiss, K., & Stringer, D. A. (1971) The skeleton: Its structure and metabolism. In D. J. Bell & B. M. Freeman (eds.), *Physiology and biochemistry of the domestic fowl*. Vol. 2. London: Academic Press. pp. 621–639.

Tully, T. N. (ed.) (2002) *The veterinary clinics of North America: Exotic animal practice*. Vol. 5, Orthopedics. Philadelphia: WB Saunders. Basic avian bone growth and healing; pp. 23–31.

Welty, J. C. (1982a) Skin scales, feathers and colours. In *The life of birds*, 3rd edn. Philadelphia: Saunders College Publishing. pp. 29–63.

Welty, J. C. (1982b) Blood, air and heat. In *The life of birds*, 3rd edn. Philadelphia: Saunders College Publishing. pp. 130–156.

West, N. H, Lowell Langille, B., & Jones, D. R. (1981) Cardiovascular system. In A. S. King & J. McLelland (eds.), *Form and function in birds*. Vol. 2. London: Academic Press. pp. 235–341.

7

Introduction to small mammals

INTRODUCTION

Mammals obviously need no introduction to any veterinary surgeon! This section is intended to revise the main morphological and physiological differences between reptiles, birds and mammals.

Mammals are endothermic, with tactile vibrissae and a pinna for collecting sound. The skin has hair modified into fur, spines, wool, and even scales. Sebaceous glands prevent water loss while sweat glands play a role in insulation through evaporation of water and salts. They have separate reproductive and excretory passages and, except for the more primitive monotremes, no cloaca. They have loops of Henle, which enable them to produce concentrated urine, and the end point of nitrogenous waste is urea. Marine mammals do not have salt glands but osmoregulate and excrete salt via their kidneys (King & Custance 1982; Vaughan 1986b).

It is thought that the high mammalian body temperature is too high for sperm development so the testes migrate outside the body to a cooler location in the scrotum. In placental mammals the lower oviduct is modified into a uterus where the embryo is nourished. Three types of uterus are found (Fig. 7.1). The primitive duplex uterus found in the rabbit, rat, and hamster has two separate branches and separate cervices uniting at the vagina. In most mammals like carnivores (dog and cat), guinea pigs, and ungulates the distal part of the uterus fuses into a uterine body to form the bicornuate or bipartite (slight partition remaining) state. The most advanced form is found in primates where there is total fusion of the uterine body, forming what is paradoxically called the simplex state (King & Custance 1982).

The heart is completely divided into four chambers, which enables the maintenance of a high blood pressure. The aortic arch curves to the left in mammals. They have a diaphragm that separates the abdomen from the thorax and extensive nasal turbinates to aid in thermoregulation. The hard palate is complete, dividing the nasal cavity from the oral cavity and allowing the animal to chew while breathing. This clear division of labor is essential for animals of high metabolic rate and it also enables the young to breathe while suckling.

Mammals have a specialized atlas–axis complex to help them rotate their head up and down and side to side. Ribs are restricted only to the thoracic vertebrae, thus enabling them to twist their lumbar spine in dorsoventral flexion. The skull has a large double occipital condyle and the adductor jaw muscles, which open the mouth, are divided into the *masseter* and the *temporalis* (King & Custance 1982). The temporal fossa provides attachment for the temporalis while the masseter inserts on the zygomatic arch. Carnivores have well developed temporal muscles while in herbivores the masseter muscle is the main muscle of mastication and the jaw articulation lies dorsal to the occlusal surfaces of the teeth (Crossley 2003) (Fig. 7.2). This enables herbivorous mammals like rabbits to have the side to side, forward, backward, and rotary chewing actions that grind down grasses. The mandible is formed from a single dentary bone to allow for insertion of these powerful muscles; the quadrate and articular bones have become the ear ossicles, incus, and malleus respectively (King & Custance 1982).

TAXONOMY

Order Carnivora

The order of carnivores consists of ten families with over 270 species and are found naturally everywhere, apart from Australia, New Zealand, Antarctica and many oceanic islands. They range in size from the tiny Least weasel (*Mustela nivalis*) which weighs 35–70 g to the grizzly brown bear (*Urus arctos*) which can weigh up to 780 kg (Nowak 1999a).

The term carnivore derives from the Latin *carnis* (flesh) and *vorare* (devour) in keeping with the fact that most species are meat eaters. However many bears are omnivorous and the Giant Panda is in fact a strict herbivore.

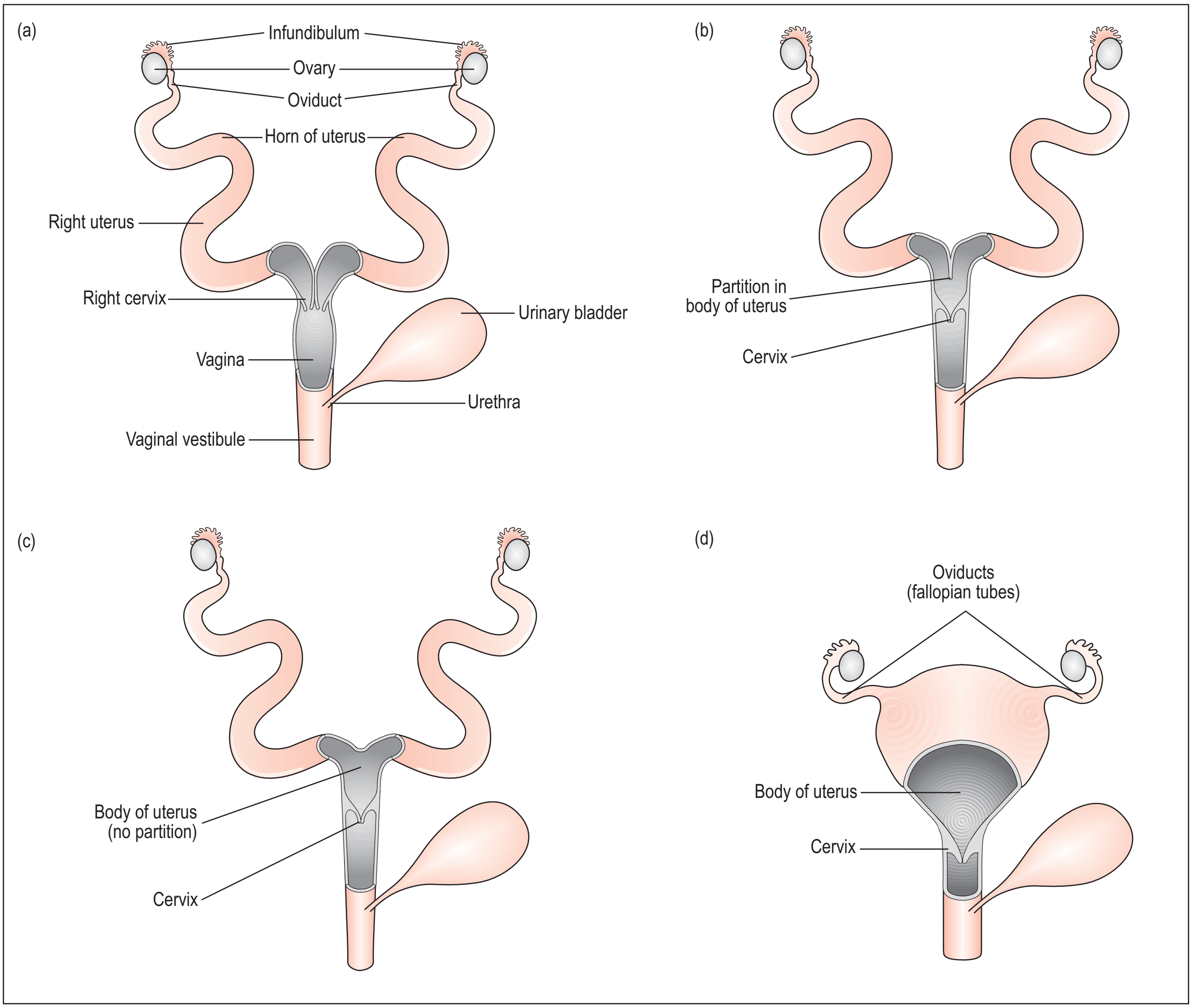

(a)
Infundibulum
Ovary
Oviduct
Horn of uterus
Right uterus
Right cervix
Urinary bladder
Vagina
Urethra
Vaginal vestibule
(b)
Partition in body of uterus
Cervix
(c)
Body of uterus (no partition)
Cervix
(d)
Oviducts (fallopian tubes)
Body of uterus
Cervix

Figure 7.1 • Types of uterus found in placental mammals.
(a) Duplex (rabbit, hamster, rat)
(b) Bipartite (some carnivores and ungulates)
(c) Bicornuate (cat, dog, ferret, and ungulates)
(d) Simplex uterus (primates)

The heavy skull has a conspicuous saggital crest with well-developed temporal muscles and a large braincase (Fig. 7.2). The jaw articulation is in the dorso-ventral plane with limited transverse movement and no rotary movement. All teeth are rooted. Most species have 3/3 incisors with large conical canines and a variable amount of shearing and crushing premolar and molars. In most carnivores the fourth upper premolar and first lower molar are carnassial teeth that work together to provide the specialized shearing action for tearing at prey when feeding (Vaughan 1986a; Nowak 1999a).

Unlike lagomorphs and rodents, carnivores are typical predators and most species have excellent hearing, vision and smell for hunting. They have large auditory bullae and well-developed turbinates and olfactory epithelium.

They have 4–5 clawed digits on each limb. The first digit is not opposable and is often absent. Many, like canids and felids are digitigrade walking on their toes while Ursids, or bears, are plantigrade walking on the soles with heels touching the ground. Young are born blind and helpless but with a covering of fur and there is usually a high level of parental care (Vaughan 1986a; Nowak 1999a).

Order Lagomorpha and Rodentia

Rodents comprise the largest mammalian order with over 1800 species (40% of all mammals) (Hurst 1999). They can be found worldwide from the Arctic to tropical and temperate regions (Nowak 1999b, 1999c). Lagomorphs

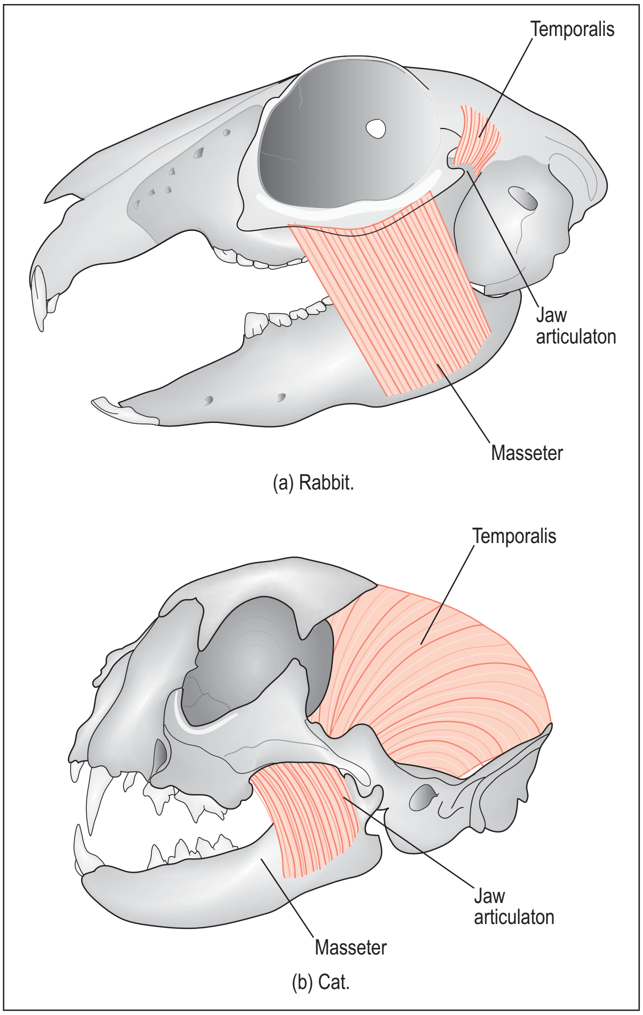


Figure 7.2 • Comparison of muscles of mastication between herbivores and carnivores. In herbivores the masseter is the main muscle of mastication and the jaw articulation lies dorsal to the occlusal surfaces of the teeth.
(a) Rabbit
(b) Cat

differ from rodents in that they have four upper incisors (Vaughan 1986c) and a different jaw structure, but otherwise they share many similar behavioral and anatomical characteristics and will be included with rodents for this introductory section (Table 7.1).

Table 7.1 Classification of Lagomorphs and Rodents

Order	Suborder	Description	Species examples
Lagomorpha			Rabbits, hares, cottontails
Rodentia	Myomorpha	Mouse like	Rats, mice, hamsters
	Caviomorpha	Cavy like	Guinea pigs, chinchilla
	Sciuromorpha	Squirrel like	Squirrels, chipmunks, prairie dogs

Lagomorphs

Rabbits belong to the order Lagomorpha, which contains two families: the Ochotonidae, which includes the pikas (Ochotona), and the Leporidae, containing rabbits and hares (Lepus) and cottontails (Sylvilagus) (Nowak 1999c).

Lagomorphs differ from rodents in both dentition and jaw structure. Unlike rodents they have two rows of upper incisors and the upper maxillary arcades lie further apart than the mandibular arcades, meaning that only one side of the cheek teeth can be occluded at a given time. Up until the mid-twentieth century they were classified as a suborder of the order Rodentia but it is now thought that their different dentition and jaw structure makes them more similar to artiodactyls, such as cows and horses (Crossley 2003; Nowak 1999b).

Rabbits differ from hares in having a short gestation period (28–33 days) and giving birth to altricial young in burrows underground. Hares are generally larger than rabbits, have a gestation period of 40 to 50 days, and give birth over ground to precocious young (Harkness & Wagner 1995; Nowak 1999c).

Rodents

Traditionally the order Rodentia was divided into the suborders Myomorpha, Sciuromorpha and the Caviomorpha (Hystricomorpha) based on skull and jaw musculature (Hurst 1999; Nowak 1999b) (Fig. 7.4). The classification of rodents is always in flux, however. More recent research on mandibular anatomy has suggested classifying rodents into just two suborders: Sciurognathi (sciuromorphs and myomorphs) and Hystricognathi (caviomorphs) (D'Erchia et al. 1996; Nowak 1999b; Vaughan 1986b).

Myomorphs

The Myomorpha, or mouse-like rodents, are the biggest suborder and include the rat, hamster, and gerbil (Fig. 7.5). They have a total of 16 teeth with no premolars, and rooted molars. Famous for their gnawing ability, a feature of this suborder is that part of the medial masseter muscles inserts not only on the lower jaw but runs through the infraorbital foramen to insert on the rostral muzzle. This unique architecture allows a more forward thrust of the jaw and more effective gnawing (King & Custance 1982; Nowak 1999b; Vaughan 1986b).

Two families from the order of Myomorpha will be featured in this book: the family Muridae, which includes rats and mice, and the family Cricetidae, which includes gerbils and hamsters. The main anatomical characteristics distinguishing these two families is that the Cricetidae have molar cusps arranged in two parallel longitudinal rows while the Muridae have cusps arranged in three rows.

Sciuromorphs

These are the squirrel-like rodents and include the chipmunk, squirrel, and prairie dog (Fig. 7.6). They have 20–22

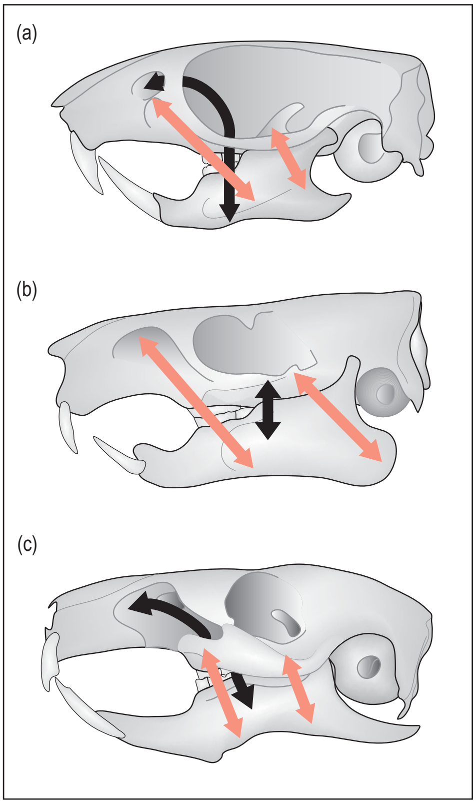


Figure 7.4 • Differing action of lateral and medial masseter muscles in rodents. Black = medial masseter. Red = lateral masseter.
(a) Myomorph – the medial masseter muscles insert not only on the lower jaw but run through the infraorbital foramen to insert on the rostral muzzle. This allows greater gnawing power
(b) Sciuromorph – these have the lateral masseter muscle extending cranially to aid gnawing. The medial masseter muscle is only involved in closing the jaw
(c) Caviomorph – the medial masseter muscles provide the gnawing action while the lateral masseter serves to close the jaw.

Figure 7.6 • Sciuromorph – Gray squirrel (*Sciurus carolinensis*).

teeth and, like the myomorphs, their molars are rooted. The sciuromorphs have the lateral masseter extending cranially and the medial masseter muscle is only involved in closing the jaw (Hurst 1999). The eyes are large as they are mainly diurnal. The tail varies from short to long and is usually haired and bushy, with long hairs that project at right angles from the tail (Nowak 1999b).

Caviomorphs (Hystricomorphs)

The suborder Caviomorpha include the guinea pig and chinchilla, which eat a highly abrasive herbivorous diet (Fig. 7.7). They have 20 teeth in total and their open rooted (aradicular) molars make them especially prone to dental disease. They also produce precocious young and have a long gestation period. In contrast to the sciuromorphs, the medial masseter muscles provide the gnawing action while the lateral masseter serves to close the jaw (Hurst 1999; Nowak 1999b).

THERMOREGULATION

Many rodents are semi-fossorial, using underground burrows and nests to either protect them from snow or help them escape from the hot sun. This enables them to survive even in extreme climates.

Figure 7.5 • Myomorph – Mouse (*Mus musculus*).

Figure 7.7 • Caviomorph – Chinchilla (*Chinchilla laniger*).

Adaptations to cold

Rodents cope with extreme cold by tunneling underground, nest building, and huddling together to conserve heat. Some species hibernate when the temperature drops but others can survive in the warm microclimate that exists between the ground and insulating layers of snow. Rodents also have elaborate adaptive mechanisms of high activity to produce heat, shivering of skeletal muscles and, most importantly, production of heat by layers of brown fat (non-shivering thermogenesis). Peripheral vasoconstriction of extremities like the tail and ears also helps divert heat to important parts of the body (Hart 1971).

Non-shivering thermogenesis

Brown fat produces heat in cold conditions because it has a rich blood supply and mitochondria capable of functioning even at very low temperatures. It is also unaffected by nutrition. This type of fat contains multiple droplets and appears brown due to its extensive capillary network (4 to 6 times that of white fat). It is under the control of the sympathetic nervous system via noradrenaline (Girardier 1983).

In rodents brown fat can be found above the scapulae, in the cervical region, and also along major vessels and nerves. It also contributes 5% of body weight in neonates. In rodents it can persist for life, with those living in cold regions laying down more tissue; for example, rats adapted to cold climates develop 1.4% of the body mass as brown fat (Hart 1971; Girardier 1983).

Brown fat is also essential for rodents that hibernate. Endothermy is very energy expensive so during winter, when food is scarce, some rodents switch this off by hibernating. At the end of the dormant period they are able to kick start their rapid metabolism via the sympathetic nervous system. Noradrenaline stimulates brown fat to heat the blood running through it, releasing energy to the brain and heart to get the body up and running again (Hart 1971; Girardier 1983).

Adaptations to heat

In hot deserts rodents build extensive underground burrows for shade, and many are nocturnal to escape the daytime heat. Many species have a marked ability to conserve water by concentrating their urine; some desert species are able to exist on metabolic water alone. Evaporation of saliva, which is groomed over the body, is also used to cool down. Like wading birds, rodents also have arteriovenous shunts with countercurrent heat exchanges in ears, tails, and feet to help them dissipate excess heat (Hart 1971).

Size

Their small size means rabbits and rodents have a high ratio of surface area to body weight and consequently a high metabolic rate and energy intake (Hurst 1999) (Fig. 7.3). This means they are easily susceptible to dehydration and hypothermia. Their fast metabolism means they have high oxygen and energy demands, making them prone to hypoglycemia and hypoxia.

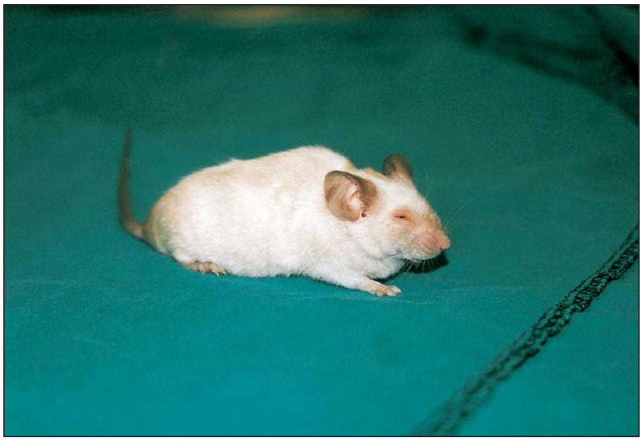


Figure 7.3 • Their high ratio of surface area to body mass means that rodents easily get dehydrated and hypothermic.

DENTITION

Most rodents have between 16 and 22 teeth but have only one pair of upper incisors, whereas rabbits have 28 teeth and two pairs. There are no canine teeth and the space between the incisors and molars is called the *diastema* (Fig. 7.8). The incisor teeth are open rooted (aradicular) and constantly grow from the base, producing a tooth like the segment of a circle. The outer surface is harder than the inner dentin, so this creates the chisel-shaped self-sharpening edge. There is no nerve in the tooth except at the base. When the rodent is gnawing, cheek folds can be pulled into the diastema and this enables the animal to gnaw at hard objects without swallowing sharp material (Hurst 1999; Nowak 1999b, 1999c; Vaughan 1986b, 1986c; Wiggs & Lobprise 1995).

The cheek teeth are composed of hard enamel covering the outer layer and some internal loops surrounding a center of softer dentine. The enamel, being harder, wears more slowly and this results in the creation of ridges on the crown of the teeth, the patterns of which aid in the classification of rodent species. Herbivorous species that feed on coarse vegetation, such as the rabbit, guinea pig, and chinchilla, have open rooted (aradicular) molars that are constantly ground down by attrition. In contrast, omnivores like the rat have molars that cease growing at 4 months (Hurst 1999; Nowak 1999b; Wiggs & Lobprise 1995).

GNAWING

The name rodent derives from the Latin *rodere*, which means to gnaw. Rabbits, and especially rodents, have large

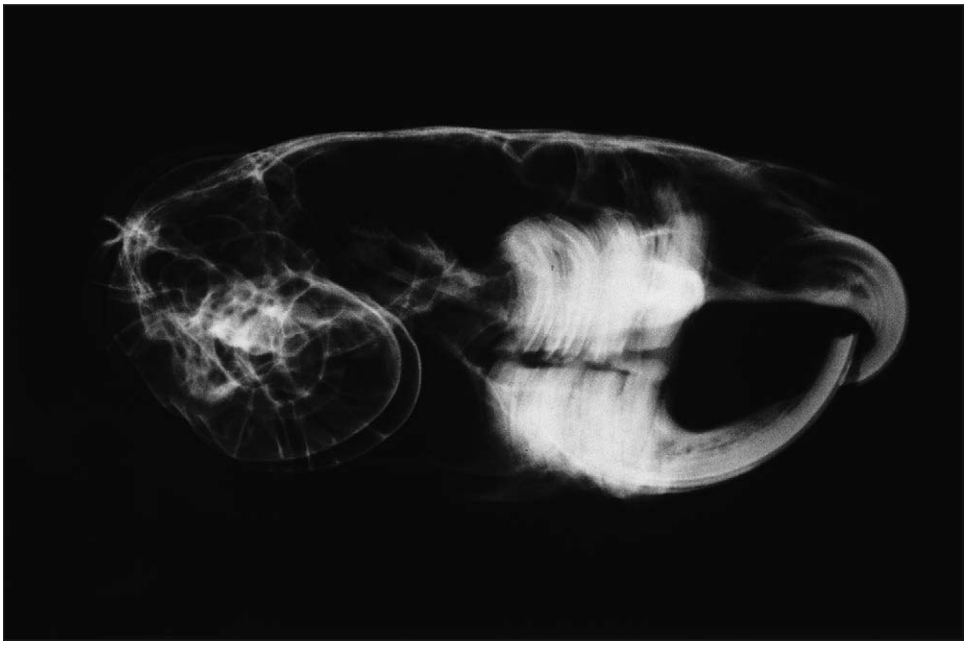


Figure 7.8 • Radiograph of chinchilla skull showing incisors, diastema and molars with large tympanic bullae. Caviomorphs have constantly growing molars as well as incisors so are very prone to dental problems.

masseter muscles that allow them great masticatory and gnawing power. The jaw articulation is loose, creating a rotary movement and enabling it to move forward and backward. This means that when the incisors are in apposition the cheek teeth are not, and vice versa. This facilitates a clear division of labor between the teeth used for gnawing and those used for grinding food (King & Custance 1982; Nowak 1999b, 1999c; Vaughan 1986b, 1986c).

COPROPHAGY

Coprophagy (from the Greek "to eat dung") is a behavior where an animal reingests its own excreted feces and it has been observed in the rabbit, rat, mouse, hamster, guinea pig, and chinchilla. It is more correctly called *cecotrophy*. While herbivorous hindgut fermenters like the rabbit, guinea pig, and chinchilla show very active cecotrophy, it is exhibited to a lesser extent in the more omnivorous rat, mouse, and hamster. It can increase during pregnancy and lactation in order to increase the supply of vitamin B12 and folic acid. Although modern diets mean that coprophagy is unnecessary for survival, it is an innate behavior stimulated by anal reflex (Ebino 1993).

REPRODUCTION

Rodents reproduce rapidly and have large litter sizes (Fig. 7.9). The myomorphs and sciuromorphs have short gestation periods (16–18 days in hamsters) and give birth to altricial young. These are rapidly weaned at 6–10 weeks and often capable of reproducing themselves in the same season (Hurst 1999).

RESPIRATION

The larynx is placed high in the oropharynx where it can directly access the nasopharynx so all these species are obligate nose breathers (Vaughan 1986b) (Fig. 10.13). Being animals of small body weight they have higher oxygen demands than larger mammals. Increased oxygen intake is facilitated not by larger lungs but by a number of other modifications.

Rabbits and rodents have high chest wall compliance and vital capacity and low residual lung capacity. This enables

Figure 7.9 • Rabbits and rodents have phenomenal reproductive rates – these Mongolian gerbils (*Meriones unguiculatus*) can start breeding from 10–12 weeks and reproduce every 26 days!

them to expand their lungs well to draw in more oxygen and expel maximum air with each breath. They also have more alveoli of thinner diameter to allow maximum oxygen exchange. For example the diameter of the alveoli of the Syrian hamster is 35-75 Um in contrast to 200 in the cat and 400 in the sedentary sloth. Shorter airways and high respiration rates also increase oxygen intake (Donnelly 1990).

SENSES

These are prey animals, so are mainly active at low light. They have an acute sense of smell, hearing, and touch (Hurst 1999), which is enabled by their possession of large tympanic bullae, sensitive vibrissae, and large olfactory bulbs in the brain. Odors form a vital means of communication and identification via pheromones in urine, feces, and scent glands. Rodents are also sensitive to ultrasound frequencies up to 150 kHz (Hurst 1999).

KEY POINTS

Rabbits and Rodents

- Acute sense of hearing, smell, and touch
- High surface area to body weight – resulting in susceptibility to rapid dehydration and hypoglycemia
- Fast metabolism – resulting in high oxygen and food intake
- Constantly growing molars in rabbits, guinea pigs, and chinchillas – hence increased incidence of dental problems in these species
- Larynx placed high in oropharynx making them obligate nose breathers
- Cecotrophy is normal behavior (especially in herbivores)

REFERENCES

Crossley, D. A. (2003) Oral biology and disorders of lagomorphs. *Veterinary Clinics of North America Exotic Animal Practice* 6(3), 629–659.

D'Erchia, A. M., Gissi, C., Pesole, G. et al (1996) The guinea pig is not a rodent. *Nature 381*, 597–599.

Donnelly, T. (1990) Rabbits and rodents. *Laboratory animal science, University of Sydney Proceedings 142: Anatomy and physiology*. Sydney, NSW: University of Sydney. pp. 369–381.

Ebino, K. Y. (1993) Studies on coprophagy in experimental animals. *Experimental Animals (Tokyo) 42*(1), 1–9.

Girardier, L. (1983) Brown fat: An energy dissipating tissue. In L. Girardier & M. J. Stock (eds.), *Mammalian thermogenesis*. London: Chapman & Hall. pp. 50–91.

Harkness, J. E., & Wagner, J. E. (1995) Biology and husbandry – the rabbit. *The biology and medicine of rabbits and rodents*, 4th edn. Baltimore: William & Wilkins. pp. 13–30.

Hart, J. S. (1971) Comparative physiology of thermoregulation, Rodents. In G. C. Causey (ed.), *Mammals*. Vol. 2. New York: Academic Press. pp. 2–130.

Hurst, J. L. (1999) Introduction to rodents. In T. Poole (ed.), *The UFAW Handbook on the care and management of laboratory animals*, 7th edn. Vol. 1. Oxford: Blackwell Science. pp. 262–274.

King, G. M., & Custance, D. R. (1982) *Colour atlas of vertebrate anatomy*. Oxford: Blackwell Scientific. The rat; pp. 6.1–6.18.

Nowak, R. M. (ed.) (1999a) *Walker's mammals of the world*, 6th edn. Vol. 11. Baltimore: John Hopkins University Express. Order Carnivora; pp. 632–634.

Nowak, R. M. (ed.) (1999b) *Walker's mammals of the world*, 6th edn. Vol. 11. Baltimore: John Hopkins University Express. Order Rodentia; pp. 1243–1244.

Nowak, R. M. (ed.) (1999c) *Walker's mammals of the world*, 6th edn. Vol. 11. Baltimore: John Hopkins University Express. Order Lagomorpha; pp. 1715–1721.

Nowak, R. M. (ed.) (1999d) *Walker's mammals of the world*, 6th edn. Vol. 11. Baltimore: John Hopkins University Express. Leporidae; pp. 1729–1731.

Vaughan, T. A. (ed.) (1986a) *Mammology*, 3rd edn. Philadelphia: Saunders College Publishing. Order Carnivora; pp. 154–161.

Vaughan, T. A. (ed.) (1986b) *Mammology*, 3rd edn. Philadelphia: Saunders College Publishing. Order Rodentia; pp. 244–277.

Vaughan, T. A. (ed.) (1986c) *Mammology*, 3rd edn. Philadelphia: Saunders College Publishing. Order Lagomorpha; pp. 277–283.

Wiggs, R. B., & Lobprise, H. B. (1995) Dental anatomy and physiology of pet rodents and lagomorphs. In D. A. Crossley & S. Penman (eds.), *BSAVA Manual of small animal dentistry*. Gloucester, UK: BSAVA. pp. 68–74.

8

Rabbits

INTRODUCTION

Origins of the rabbit

The rabbit (*Oryctolagus cuniculi*) originally came from the Iberian peninsula but was introduced to the rest of Europe over 2000 years ago by the Romans who kept them in walled gardens called *leporaria*. They were further domesticated by French monks from the 5th to 6th centuries onwards who feasted on the "aquatic young" in place of meat during Lent (Batchelor 1999; Nowak 1999b). In the 12th century the Normans brought the rabbit to England and Ireland and they became common during the following two hundred years. They were fully domesticated by the 17th century, initially being used for game on the landlords' estates, but they became a popular source of food during the era of industrialization (Batchelor 1999; Sandford 1996). In the Victorian era the rabbit became popular as a children's pet and entered the realms of fiction in books like Alice in Wonderland, Peter Rabbit, and Brer rabbit. During the two world wars there were also mini-booms in keeping rabbits for food when other sources of food were scarce (Sandford 1996).

As it spread throughout Europe, the rabbit was such a successful breeder that the early explorers carried it as a food source and released it on remote oceanic islands. It was introduced to South America in the mid-18th century and to Australia and New Zealand in the late 19th century, where the absence of predators meant it rapidly reached pest proportions (Bell 1999). Although released in North America it – fortunately for farmers – never managed to survive there in the wild (Sandford 1996).

There are now over 70 recognized breeds of fancy and Rex rabbits (Batchelor 1999) and it is ever popular as a pet, and also for farming and laboratory research. The first set of experiments on rabbits was in 1852 when an Austrian physician fed deadly nightshade to rabbits and found that 60% of them showed no ill effects (Brewer & Cruise 1994; Stein & Walshaw 1996). This led to the discovery of the rabbit enzyme atropinesterase that hydrolyses atropine, thereby reducing the effect of atropine in this species. The two parts of the taxonomic name of the rabbit, *Oryctolagus cuniculus*, translate from the Latin as "burrowing hare" and "underground passage", respectively.

Longevity and size

The average life span of rabbits is 7–10 years. They vary in size, depending on breed, ranging from the 7 kg Flemish Giant to the 1 kg Dwarf Polish or Dutch breeds (Batchelor 1999; Harkness & Wagner 1995).

THERMOREGULATION

The normal body temperature is 38.5–39.5° C (Brewer & Cruise 1994). Rabbits are extremely sensitive to heat so should be housed at between 15 and 21° C (Batchelor 1999). They cannot sweat and have an inefficient salivation and panting mechanism. In the wild, they cool down by seeking shade in their burrows or stretching out to increase body surface area. The long ears are also essential for heat dispersion, having a countercurrent arteriovenous shunt. In fact, directly cooling the ears causes a drop in body core temperature and vice versa (Brewer & Cruise 1994; Cheeke 1987c).

High temperatures also inhibit drinking and panting, which can hasten dehydration and be fatal. Rabbits are also sensitive to low humidity but, as underground burrows are naturally quite humid, high humidity levels are not a problem.

Unlike rodents, adult rabbits possess no brown fat and so they shiver when cold and retain body heat by shunting warm blood from the ears to warm the body core. They also adopt a hunched posture and huddle together to decrease the collective surface area (Cheeke 1987c).

GENERAL EXTERNAL ANATOMY

There are four main fur types. These are based on fur length and range from the Rex and Satin at 12 mm, to normal rabbits at 30 mm and the Angora rabbit at as long as 120 mm. Normal rabbits have stiff, long guard hairs with a soft underfur while Rex and Satin breeds have guard hairs as short, or shorter, than the undercoat.

There are hairless areas on the nose, part of the scrotum, and in the inguinal areas in both sexes. Rabbits do not have footpads and the toes and metatarsals are covered in coarse fur. The rabbit stands plantigrade, with the whole area from hock to toe in contact with the ground, but becomes digitigrade when running (Fig. 8.2).

Head and neck

The rabbit has long funnel-like ears and the pinna is composed of a thin layer of skin overlying elastic cartilage. It is freely movable and capable of independent action. Inside the ear canal a cartilaginous ridge, the tragus, separates the ear canal from a blind-ended diverticulum. Sebaceous glands are present in the skin. The pinnae represent 12% of the rabbit's body surface and so are a major site for heat loss and gain (Brewer & Cruise 1994; Cruise & Nathan 1994). There is a highly visible central artery and peripheral veins, which form large arteriovenous shunts when heated (Fig. 8.1).

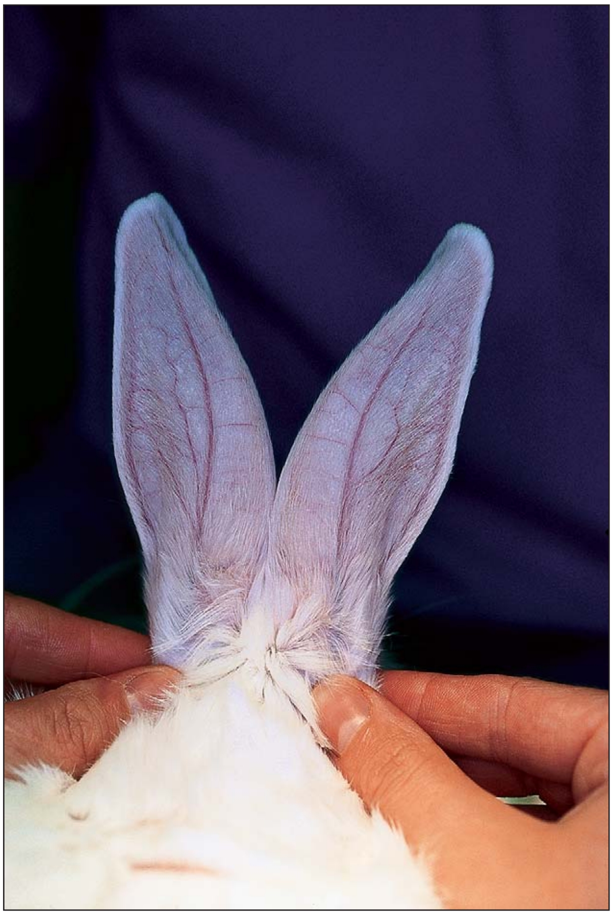


Figure 8.1 • The rabbit ears represent 12% of surface area so are a major source of heat exchange. There is a highly visible central artery and peripheral veins which form large arteriovenous shunts when heated.

There is a well-developed third eyelid, which covers the eye during anesthesia or sleep. In low light the pupils dilate widely to allow for increased retinal sensitivity (Cruise & Nathan 1994). Rabbit eyes readily detect motion and are particularly sensitive to blues and greens at twilight (Harkness & Wagner 1995). The mouth is very small. The upper lip has a median cleft or philtrum that curves to the right and left around the nose – hence the term "harelip". The neck has a pendulous skin fold called the dewlap, which is more pronounced in the doe and certain breeds (Fig. 8.2).

CLINICAL NOTE

The dewlap is often a site of wet dermatitis. This is caused by increased salivation due to dental pain, continual wetting of the skin from water bowls and poor hygiene of bedding. Obese animals, or does with large dewlaps, are more likely to suffer from this problem (Cruise & Nathan 1994).

External genitalia

The male has a rounded penile sheath and a round urethra with oblong scrotal sacs on each side. The penis can easily be extruded. The female vulva appears triangular and has a slitlike orifice (Fig. 8.3). The mammary glands (usually eight in number) are located along the thoracic and inguinal region. Only the female has nipples (Cruise & Nathan 1994). In the perineal region of both sexes there are two hairless patches lateral to the anus that contain the waxy inguinal glands.

SKELETAL SYSTEM

The skeleton of the pet rabbit is fragile in comparison with its heavy musculature (Fig. 8.4). For example, in the New Zealand White rabbit the skeleton accounts for 6%, while the muscles total 56% of body mass (Jelenko et al. 1971).

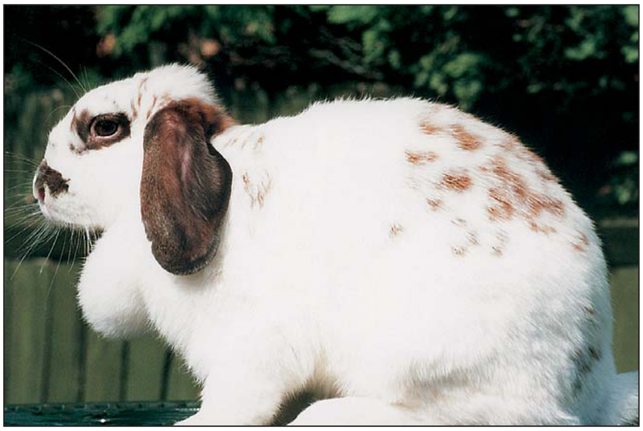


Figure 8.2 • Rabbit doe showing the dewlap, which is prone to wet dermatitis.

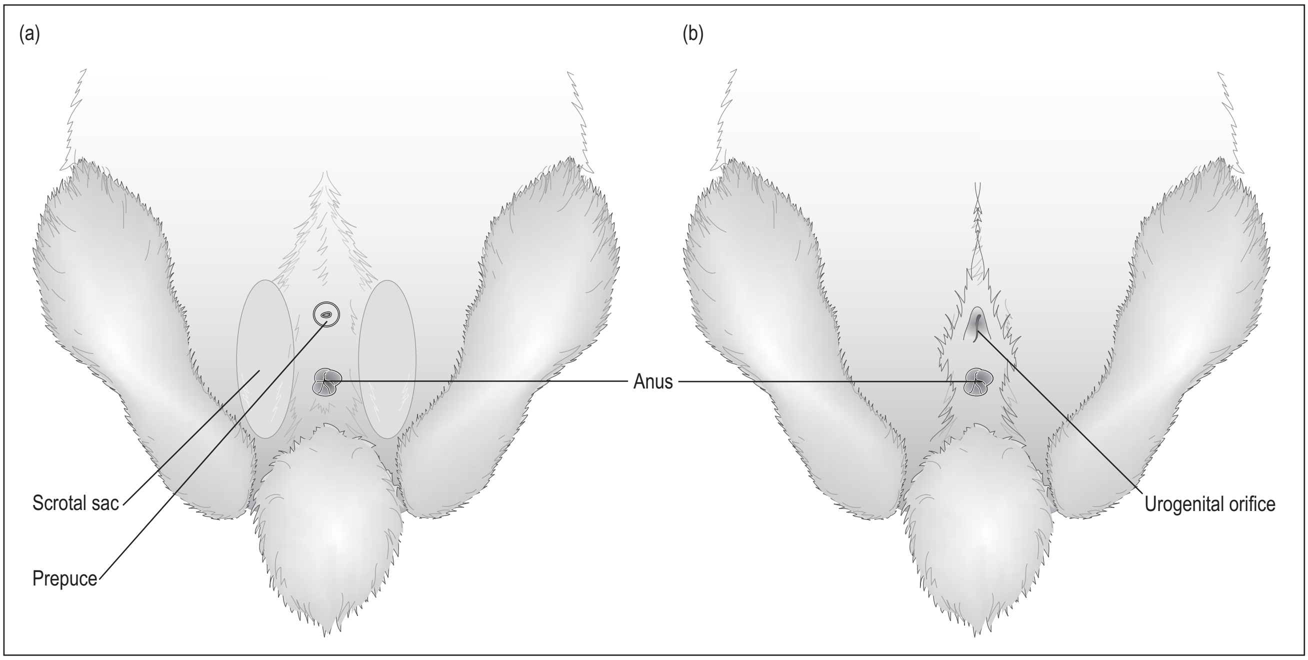

(a)
(b)
Anus
Scrotal sac
Prepuce
Urogenital orifice

Figure 8.3 • External genitalia.
(a) Male – the urethra is round and the penis can be extruded.
(b) Female – the vulva is triangular with a slitlike orifice.

If the rabbit's spine is unsupported while being handled the heavy hindquarters twist about the lumbrosacral junction to cause fractures (Harkness & Wagner 1995). L6–7 is a common site for spinal fractures, especially in young rabbits.

The vertebral formula is C7, T12–13, L7, S4, C15–16 (Cruise & Nathan 1994). The costal cartilages of the first seven ribs (true ribs) articulate with the sternum. The 7th to 9th ribs have attached costal cartilages while the 10th to 12th ribs are floating. There are seven sternebrae. The

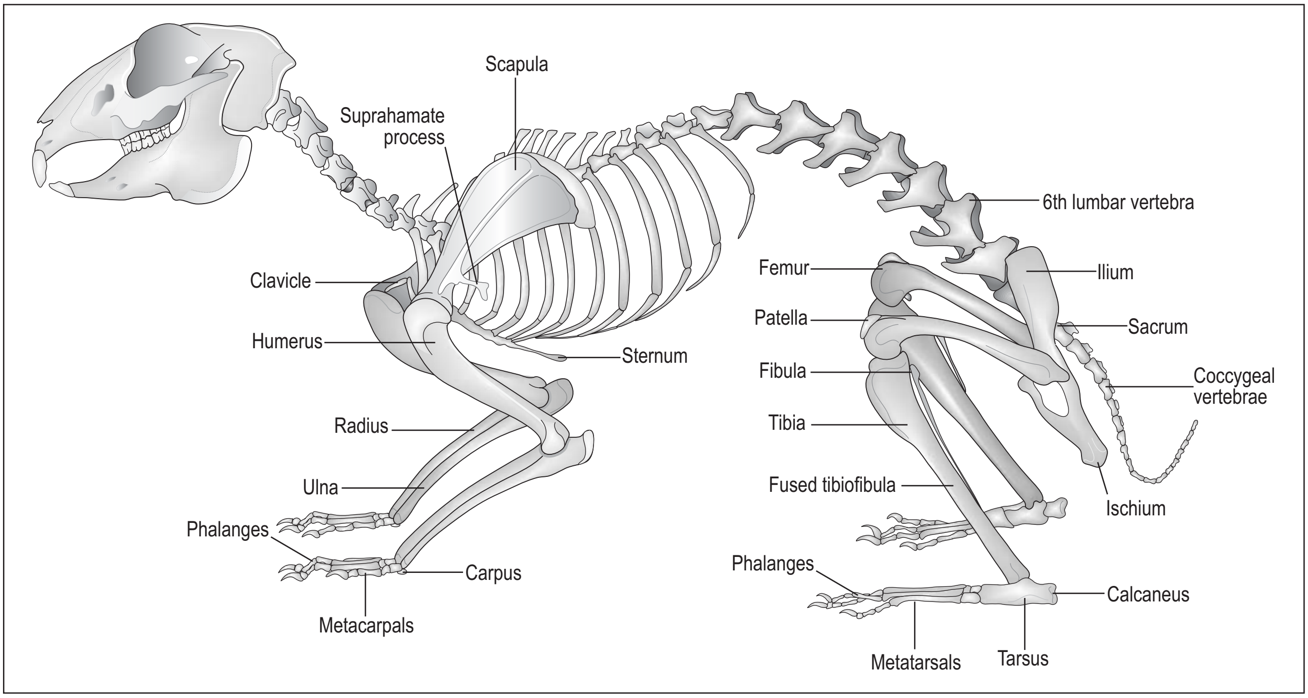

Scapula
Suprahamate process
6th lumbar vertebra
Clavicle
Humerus
Sternum
Radius
Ulna
Phalanges
Carpus
Metacarpals
Femur
Ilium
Patella
Sacrum
Fibula
Coccygeal vertebrae
Tibia
Fused tibiofibula
Ischium
Phalanges
Calcaneus
Metatarsals
Tarsus

Figure 8.4 • Skeleton of the rabbit (*Oryctolagus cuniculus*). From Popesko, P., Rajtova, V., & Horak, J. (1990) A colour atlas of anatomy of small laboratory animals. Vol. 1. Aylesbury, UK: Wolfe with permission.

transverse processes of the lumbar vertebrae are long and narrow (Okerman 1994).

The pectoral girdle contains the scapulae and small paired clavicles. The scapula has a much more triangular infraspinous fossa than that in the cat, which is more rounded. The acromion process has a bony projection jutting at right angles, which is called the *superhamate process* (Fig. 8.5) (Okerman 1994). The carpus has two rows: four bones proximally and five distally (Fig. 8.6). There are five digits and each has three phalanges, except for the first digit, which has a shorter metacarpal and only two phalanges (Cruise & Nathan 1994).

The rabbit has a small accessory bone called the *os acetabulum*, which helps form the acetabulum, along with the ischium and ilium (Cruise & Nathan 1994). The obdurator foramina are oval in shape. The femur articulates only with the tibia; the thin, blade-like fibula is fused with the tibia for over half its length (Cruise & Nathan 1994; Okerman 1994)(Fig. 8.7). There are six tarsal bones arranged in three rows: the proximal row contains the two large bones, the tarsus and calcaneus; the middle row has one central bone, and the distal row has three bones (the 2nd, 3rd, and 4th tarsal bones) (Fig. 8.8). Metatarsals 2–5 are well developed, with a rudimentary metatarsal 1. The four digits each have three phalanges (Cruise & Nathan 1994).

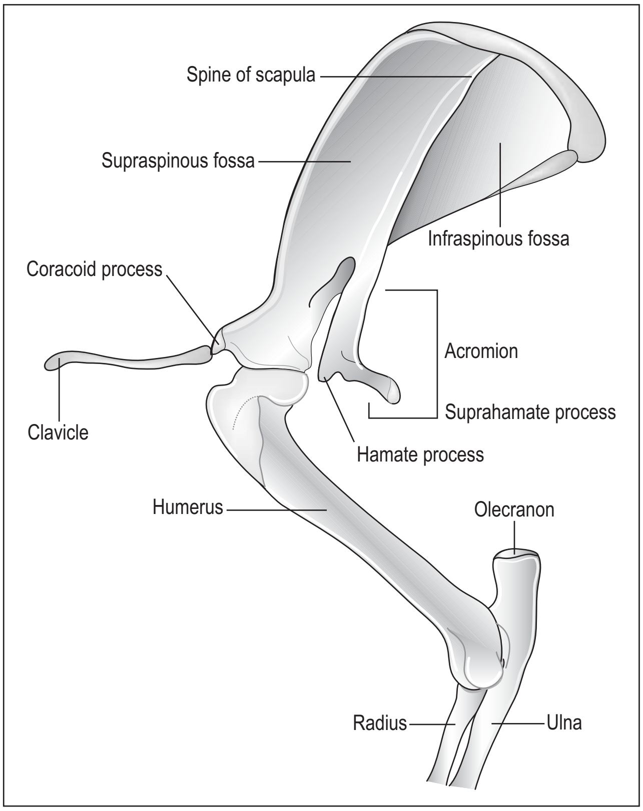

Spine of scapula
Supraspinous fossa
Infraspinous fossa
Coracoid process
Acromion
Suprahamate process
Clavicle
Hamate process
Humerus
Olecranon
Radius
Ulna

Figure 8.5 • Left shoulder of the rabbit – the acromion process has the bony superhamate process jutting at right angles. The infraspinous fossa is more triangular than in the cat. From Popesko, P., Rajtova, V., & Horak, J. (1990) A colour atlas of anatomy of small laboratory animals. Vol. 1. Aylesbury, UK: Wolfe with permission.

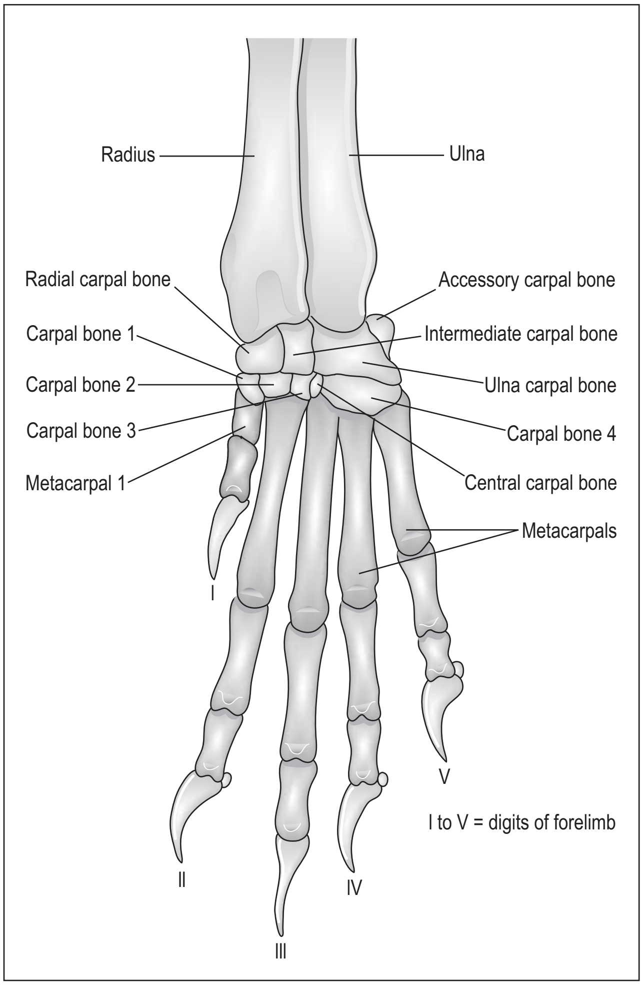

Radius
Ulna
Radial carpal bone
Accessory carpal bone
Carpal bone 1
Intermediate carpal bone
Carpal bone 2
Ulna carpal bone
Carpal bone 3
Carpal bone 4
Metacarpal 1
Central carpal bone
Metacarpals
I
V
I to V = digits of forelimb
II
IV
III

Figure 8.6 • Dorsal view of left carpus of the rabbit. From Popesko, P., Rajtova, V., & Horak, J. (1990) A colour atlas of anatomy of small laboratory animals. Vol. 1. Aylesbury, UK: Wolfe with permission.

CARDIOVASCULAR SYSTEM

The heart rate can vary from 180 to 250 beats per minute. It is relatively small and the right atrioventricular valve has only 2 cusps, making the term “tricuspid” incorrect. The pulmonary artery is thickened and more muscular than in dogs and cats. Rabbits have a simple conduction system and the sinoatrial node consists merely of a small group of cells generating impulses; this is why they were used in the first pacemaker experiments (Cruise & Nathan 1994).

Unlike the dog, which has significant anastomoses between the internal and external jugular vein, the main vessel for return of blood from the head is the external jugular vein. Therefore, damage or ligation of this vein in rabbits means the eye is subject to proptosis. The same pattern also occurs with the external and internal carotid artery (Donnelly 1997).

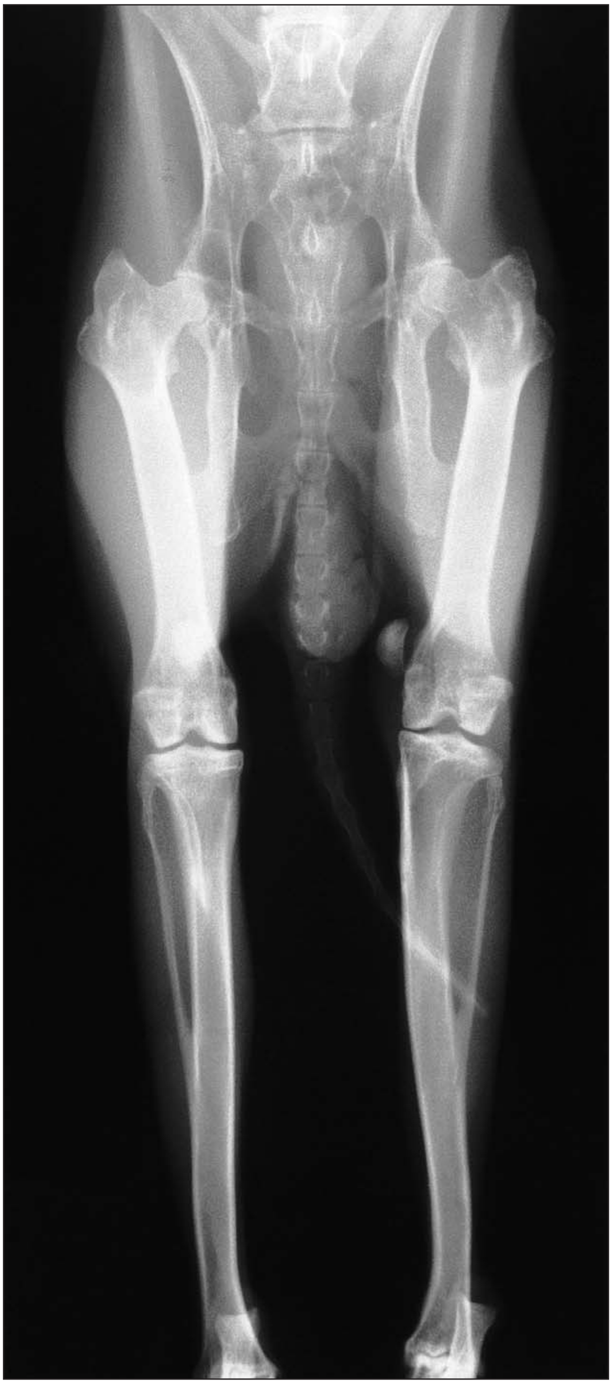


Figure 8.7 • This rabbit had a medial luxating patella of the left stifle which needed surgical correction. In rabbits there is a degree of fusion of the fibula and tibia.

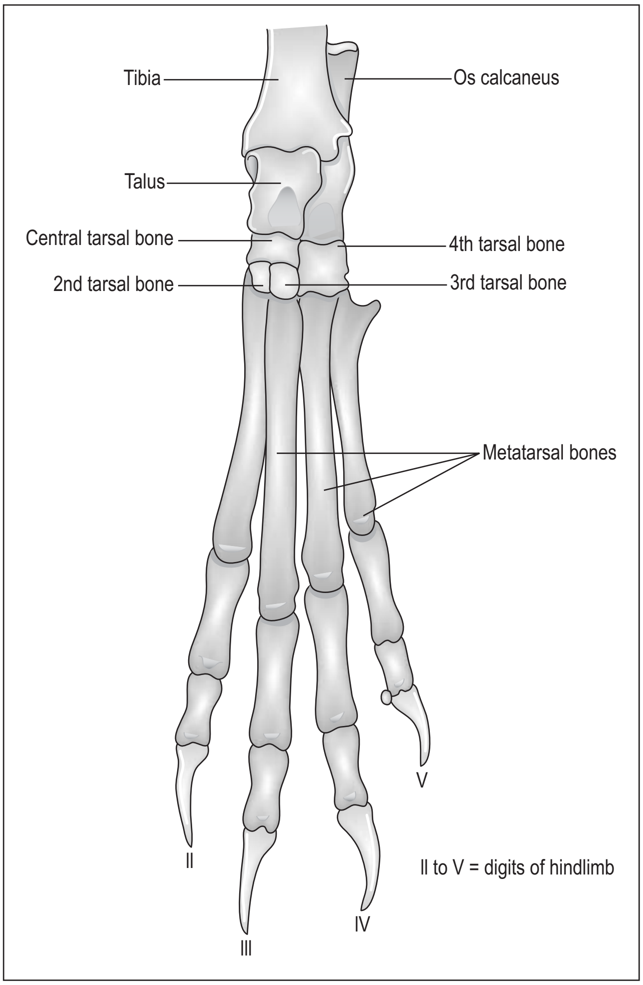


Figure 8.8 • Dorsal view of left tarsus of the rabbit. From Popesko, P., Rajtova, V., & Horak, J. (1990) A colour atlas of anatomy of small laboratory animals. Vol. 1. Aylesbury, UK: Wolfe with permission.

Venepuncture sites

The blood volume of a rabbit is 55–70 ml/kg (Benson & Paul-Murphy 1999; Donnelly 1997). For blood sampling the best sites are the central auricular artery and jugular vein. Smaller samples (<0.5 ml) can be taken from the marginal ear vein, cephalic or lateral saphenous vein, although they tend to collapse under negative pressure (Benson & Paul-Murphy 1999; Stein & Walshaw 1996).

CLINICAL NOTE

The most visible blood vessel in the ear is the central straight auricular artery. Injections or fluids into this vessel could be fatal so the smaller and less visible marginal vein should be used instead.

Blood cells

Erythrocyte life span is directly related to metabolic rate so smaller animals like rabbits and rodents have short-lived erythrocytes. Rabbit neutrophils stain pink and are called heterophils. The rabbit is unique in that is routinely has circulating basophils that can represent up to 30% of circulating leukocytes (Benson & Paul-Murphy 1999; Harkness & Wagner 1995; Percy & Barthold 2001). The lymphocyte, however, is the most prevalent white blood cell (up to 60%). Rabbits with infections do not show an elevated total white cell count but instead show a heterophilia with relative lymphopenia (Benson & Paul-Murphy 1999).

IMMUNE SYSTEM

The thymus gland remains large, even into adult life. It lies cranial to the heart and extends forward into the thoracic inlet (Cruise & Nathan 1994). The spleen is small, dark red, flat, and elongated and lies along the greater curvature of the stomach. Lymphoid tissue is present in the tonsils, sacculus rotundus, appendix, and Peyer patches in the small intestine (Cruise & Nathan 1994). This extensive gut associate lymphoid tissue (GALT) occupies 50% of all lymphoid tissue and may account for the relatively small spleen (Okerman 1994).

RESPIRATORY SYSTEM

Upper respiratory tract

There are sensory pads at the entrance of each nostril, making the rabbit very sensitive to touching that area (Nowak 1999a). There are 20 to 25 tactile vibrissae located on each side of the upper lip. The nostril twitches at a rate of 20 to 150 twitches per minute but is still when the rabbit is totally relaxed (Brewer & Cruise 1994). The turbinate bones have the vomeronasal organ and olfactory epithelium, giving rabbits their acute sense of smell. The glottis is small and often covered by the tongue. Intubation is difficult due to the small glottis, long tongue, narrow oropharynx, and laryngospasm (Brewer & Cruise 1994; Cruise & Nathan 1994).

CLINICAL NOTE

Rabbits are obligate nose breathers (Cruise & Nathan 1994) so any damage to the nares or turbinates can be serious. Avoid touching the nares because sensory pads there make them acutely sensitive to touch.

Lower respiratory tract

The thorax is small in contrast to the large abdomen (Harkness & Wagner 1995)(Figs. 8.9 and 8.10). The thymus, which persists in the adult, lies ventral to the heart and extends forward into the thoracic inlet. The lungs are divided into cranial, middle, and caudal lung lobes. The left cranial lobe is much smaller than the right due to the presence of the heart (Cruise & Nathan 1994). Rabbits have very thin pleura and, unlike other domestic mammals, there are no septa dividing the lung into lobules. Hence, pneumonia is not so localized as in other species.

The respiratory rate is 30–60 per minute. Rabbits at rest respire mainly using muscular contractions of the diaphragm and do not use their intercostal muscles for respiration (Brewer & Cruise 1994).

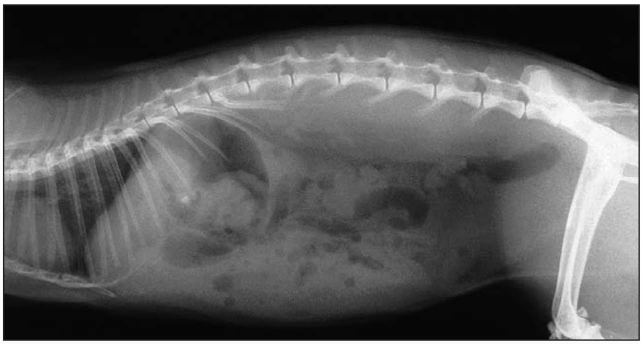


Figure 8.9 • Lateral radiograph of rabbit thorax and abdomen. Unlike carnivores, gas in the abdominal viscera is normal for herbivores.

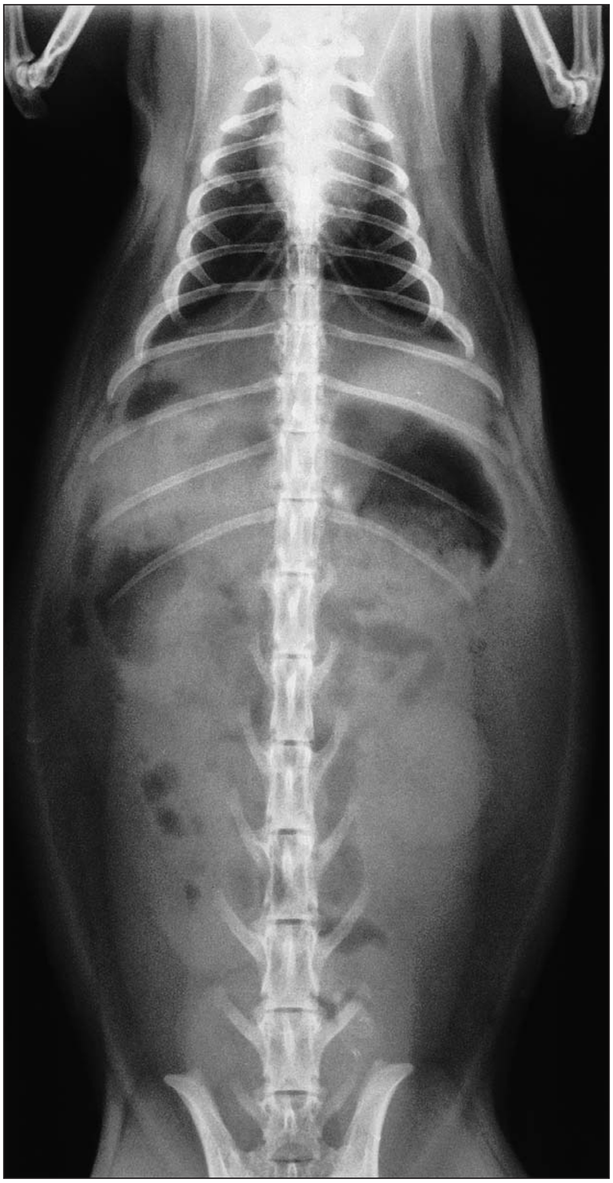


Figure 8.10 • Ventrodorsal radiograph of rabbit showing relative size of thorax and abdomen. The thorax should be raised above the abdomen during anesthesia to prevent compression from the enormous weight of the cecum.

CLINICAL NOTE

For cardiopulmonary resuscitation it is important to pull the tongue forward away from the glottis. As the diaphragm is the main muscle of respiration, hold the rabbit's head up and down every 1–2 s to stimulate diaphragmatic breathing (Brewer & Cruise 1994).

KEY POINTS

- Avoid touching nostrils as they are acutely sensitive and rabbits are obligate nose breathers.
- The spine is fragile and fractures at L6–7 are common.
- The diaphragm is the most important muscle for breathing so this must be taken into account when giving CPR.
- The thorax is small in comparison to the vast size of the abdomen, so avoid any pressure from viscera during anesthetics (Fig. 8.10).
- Neutrophils are called heterophils as they stain pink.

DIGESTIVE SYSTEM

Feeding patterns

Rabbits are crepuscular, feeding at dusk and early morning. Although they tolerate bitter food like alfalfa and thyme well, they show preference for sweet foods like molasses and sucrose (Carpenter 1956; Harkness 1990; Harkness & Wagner 1995). They eat to satisfy calorie requirements and consumption of food increases at lower temperatures (Cheeke 1987f). Conversely, it decreases at high temperatures.

The rabbit is a non-ruminant herbivore with a large hindgut. Unlike ruminants, which break down their food by chewing the cud, rabbit use browsing behavior and cecotrophy to achieve high food conversion (Cheeke 1994); this makes them the most efficient users of plant protein, converting 70 to 80% of plant protein into food (Harkness 1990; Harkness & Wagner 1995).

Browsing

Unlike the grazing horse or cow, which eats the entire plant, the rabbit selects the most nutritious part of the plant, favoring young, succulent plants over mature, coarse growth (Cheeke 1987f). This browsing behavior (also seen in giraffes and deer) helps an animal of small body weight sustain its high metabolic rate (Cheeke 1987a, 1994). Rabbits ingest coarse fiber only to stimulate gut motility and, unlike horses (which carry fiber for up to three days) rapidly excrete it, thus obviating the need to carry vast quantities around (Brooks 1997; Harkness & Wagner 1995; Jenkins 2000).

Table 8.1 Major differences in gastrointestinal tract between rabbit and ruminant (cow)

Rabbit	**Cow**
Digest cellulose	Digest cellulose
Cecal fermentation	Rumen fermentation
Main VFA is acetic acid	Main VFA is propionic acid
Low gut retention time	Holds food for 4× longer than rabbit
Bacteroides spp. microflora	*Lactobacillus* spp. microflora

VFA, volatile fatty acid

CLINICAL NOTE

Rabbits fed free choice will select concentrates (Cheeke 1987a; Harcourt-Brown 1996). This ability to select high protein and carbohydrate over fiber means that pet rabbits fed only a high concentrate diet may not get enough fiber to stimulate gut motility and will suffer consequently from intestinal stasis (Cheeke 1994).

The rabbit's hindgut consists of a vast cecum, where food is fermented, and the proximal colon, which mechanically separates the high and low fiber particles. High fiber particles are eliminated fast while the nutrient-rich particles are sent back to the cecum to be made into cecotrophs. These high fiber particles, known as the "scratch factor" in the French rabbit industry are essential for the normal functioning of the rabbit gastrointestinal process (Brooks 1997).

Prehension of food

Rabbits have a blind spot directly in front of the mouth so cannot see food placed directly there. Instead it uses its sensitive prehensile lips and vibrissae for food discrimination and prehension (Jenkins 2000; Whitehouse & Grove 1968).

CLINICAL NOTE

Rabbits do not use their incisor teeth for prehending food, so in cases of severe incisor malocclusion it is possible to extract all incisor teeth. They will no longer be able to slice their food but this is rarely a problem for the pet rabbit (Fig. 8.16).

Oral cavity

The mouth aperture is small and designed for nibbling. The rabbit's teeth are developed for the high fiber herbivorous diet. Wild rabbits have brown staining on the crowns of the teeth from feeding on natural grasses. The dental formula is 2/1,0/0,3/2, 3/3 = 28. Like all Lagomorphs, rabbits have three pairs of incisors: two upper and one lower (Crossley 2003; Vaughan 1986). The second upper incisors are rudimentary and called peg teeth and lie just behind the upper incisors. At rest, the lower incisors should rest just behind the upper incisors (Fig. 8.12).

There are no canines and the gap between the incisors and premolars is called the *diastema* (Fig. 8.11). The furred cheeks can be folded into this space, separating the incisor teeth from the oropharynx. The premolars and molars function as one unit and are often referred to as cheek teeth (Fig. 8.15). Branches of the lingual artery run close to the lower cheek teeth so must be avoided during dental surgery.

CLINICAL NOTE

Normal upper incisors have a vertical groove running along the length of the tooth and have smooth white enamel. If horizontal grooves are visible in the enamel it can be a sign of dental disease due to poor diet (Harcourt-Brown 1996, 1997).

CLINICAL NOTE

Mandibular prognathism means an abnormally long jaw relative to the length of the maxilla. It is inherited as an autosomal recessive trait and leads initially to edge-to-edge apposition and blunting of the chisel edges. Later, the lower incisors protrude rostral to the upper incisors (Fig. 8.17).

KEY POINTS

- Rabbits are highly efficient food convertors.
- Fiber is essential for gut motility.
- Browsing feeding means rabbits will selectively prefer high concentrates.
- Incisors and molars are continually growing. Malocclusion results secondary to an insufficiently fibrous and abrasive diet.

The mandible is united by a strong fibrous symphysis and is narrower than the maxilla (Fig. 8.13 and 8.14). Both incisor and molar teeth are rootless (aradicular) and constantly growing at a rate of approximately 2 mm per week. The incisors help to slice the food, which is then chewed to a bolus by the action of the cheek teeth, which along with the tongue move the bolus caudally so that all teeth get equal chewing action (Crossley 2003).

Mastication

The flexible temporomandibular joint allows the jaw to open and close and also move rostrally, caudally, and laterally (Fig. 8.11). The cheek teeth arcades function as one unit and grind the long stem fibers into small food boluses, which

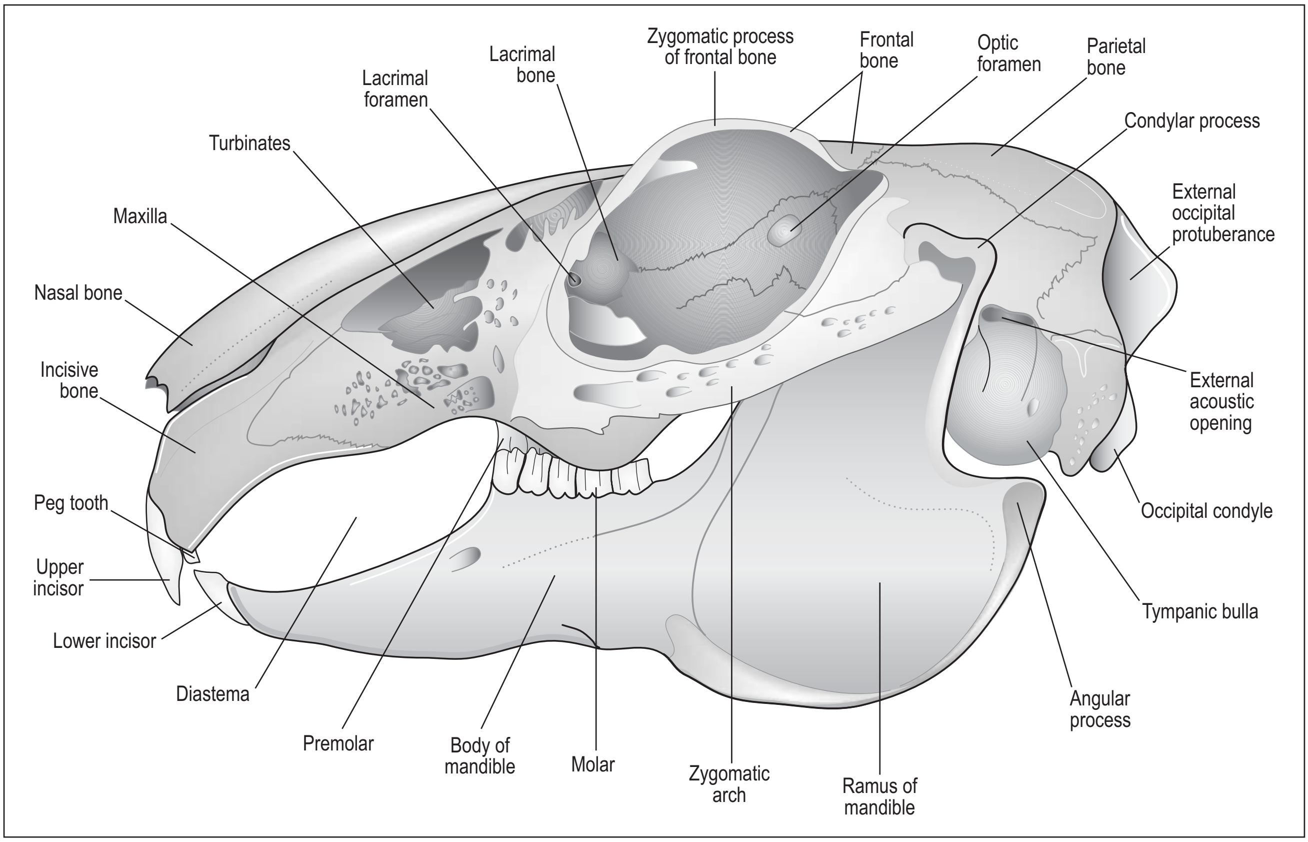

Zygomatic process of frontal bone
Frontal bone
Optic foramen
Parietal bone
Lacrimal bone
Lacrimal foramen
Turbinates
Condylar process
Maxilla
External occipital protuberance
Nasal bone
Incisive bone
External acoustic opening
Peg tooth
Occipital condyle
Upper incisor
Lower incisor
Tympanic bulla
Diastema
Angular process
Premolar
Body of mandible
Molar
Zygomatic arch
Ramus of mandible

Figure 8.11 • Lateral view of skull and mandible. From Popesko, P., Rajtova, V., & Horak, J. (1990) A colour atlas of anatomy of small laboratory animals. Vol. 1. Aylesbury, UK: Wolfe with permission.

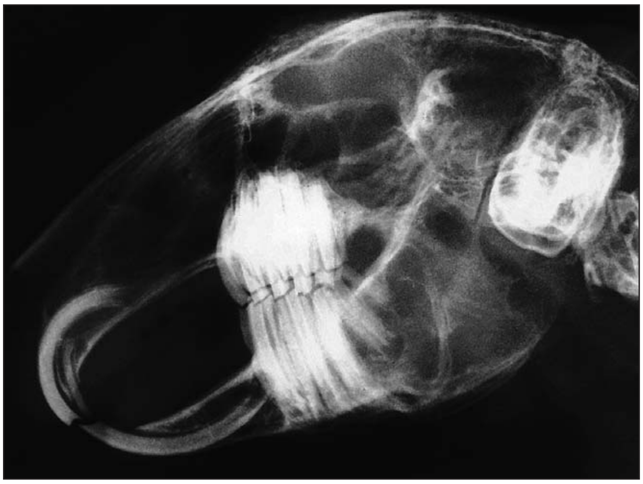


Figure 8.12 • Lateral radiograph of skull and mandible.

can then be swallowed. The jaws appose only one side at a time and rotate laterally at a rate of 120 times a minute. The tongue is utilized to make sure all food is thoroughly masticated. Cecotrophs are not chewed but swallowed intact (Brewer & Cruise 1994).

Tongue

The tongue is very long and has an elevated region caudally called the *lingual torus*. Numerous papillae along its length give it a roughened appearance. Four types are present: vallate, foliate, fungiform, and filiform; all but the last contain taste buds (Crossley 2003). Unlike the rat, the rabbits has paired tonsils.

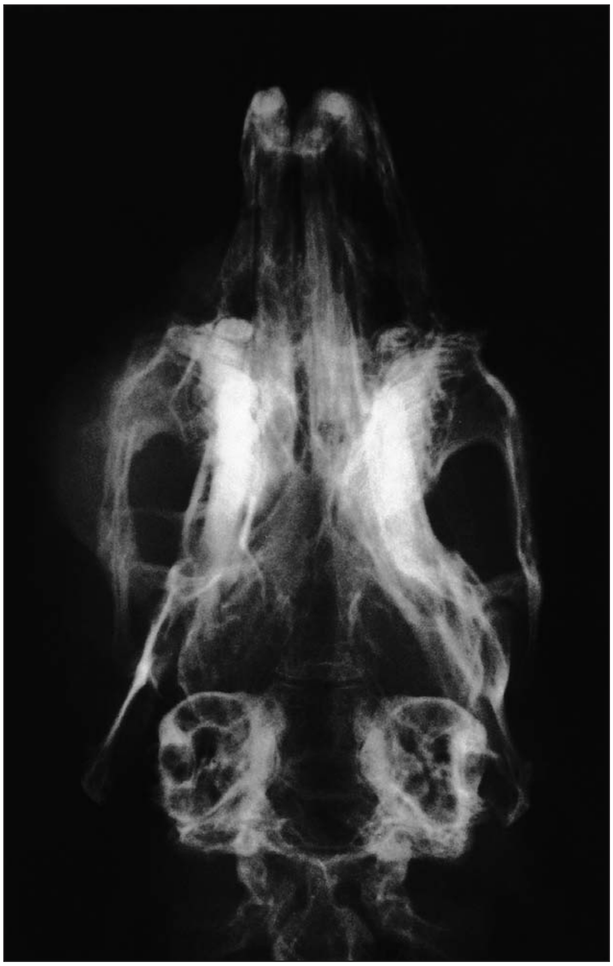


Figure 8.14 • Dorsal radiograph of skull (slightly rotated).

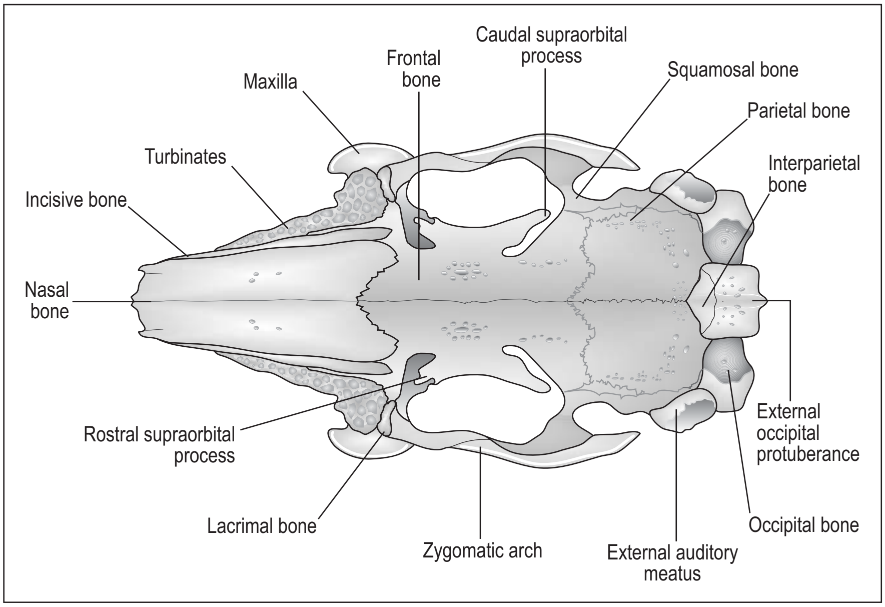

Caudal supraorbital process
Frontal bone
Maxilla
Squamosal bone
Parietal bone
Turbinates
Interparietal bone
Incisive bone
Nasal bone
External occipital protuberance
Rostral supraorbital process
Lacrimal bone
Occipital bone
Zygomatic arch
External auditory meatus

Figure 8.13 • Dorsal view of skull.

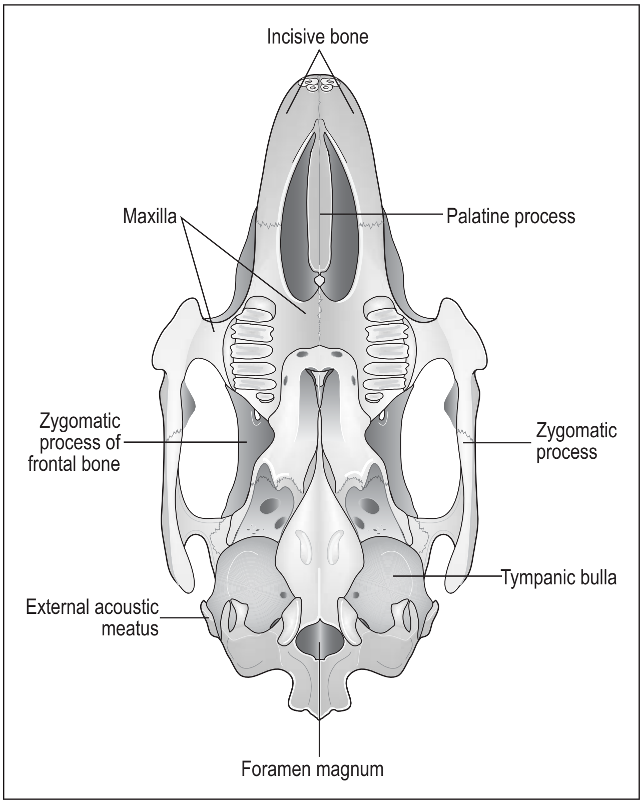


Figure 8.15 • Ventral view of skull. From Popesko, P., Rajtova, V., & Horak, J. (1990) A colour atlas of anatomy of small laboratory animals. Vol. 1. Aylesbury, UK: Wolfe with permission.

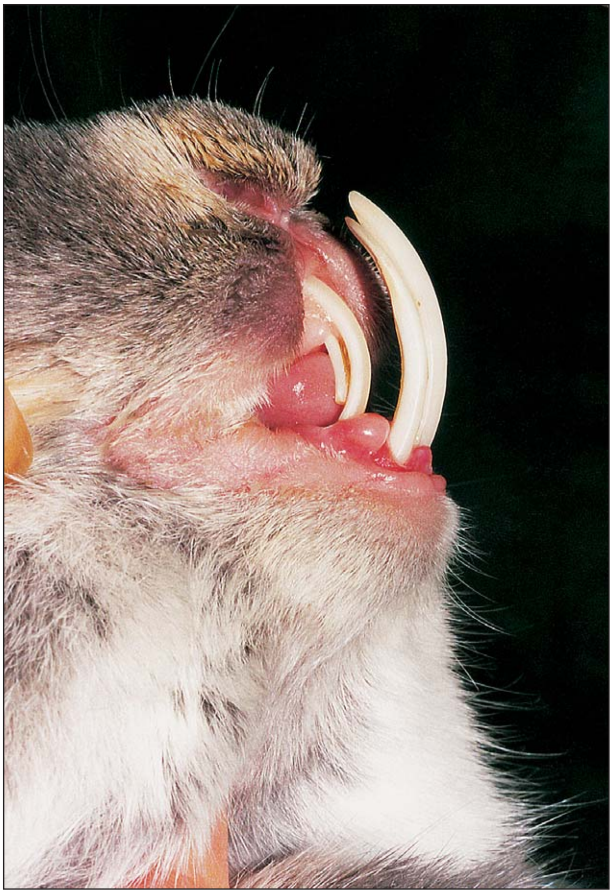


Figure 8.16 • Close up of rabbit with severe incisor malocclusion showing upper and lower incisors and peg teeth. (Photo by Claire Nuttall)

Salivary glands

There are four pairs of salivary glands: the parotid, zygomatic, mandibular, and sublingual (Jenkins 2000). The sublingual is a minor gland as the major sublingual is not present. The zygomatic gland lies just below the lacrimal gland in the anteroventral angle of the orbit (Cruise & Nathan 1994). Amylase is secreted by the glands in response to food entering the mouth (Brewer & Cruise 1994).

Esophagus

The esophagus has three layers of striated muscle, which, unlike in the dog and humans, extend all the way to the cardia of the stomach. There are no mucous glands in the esophagus. The cardia has a well-developed sphincter and is positioned so that the rabbit cannot vomit (Brewer & Cruise 1994; Cruise & Nathan 1994)(Fig. 8.18).

Abdominal cavity

Rabbit muscles are pale red in comparison to the darker red of cats and dogs (Okerman 1994). There is scant subcutaneous tissue on the midline. The linea alba is thin and lies in very close proximity to the cecum and bladder.

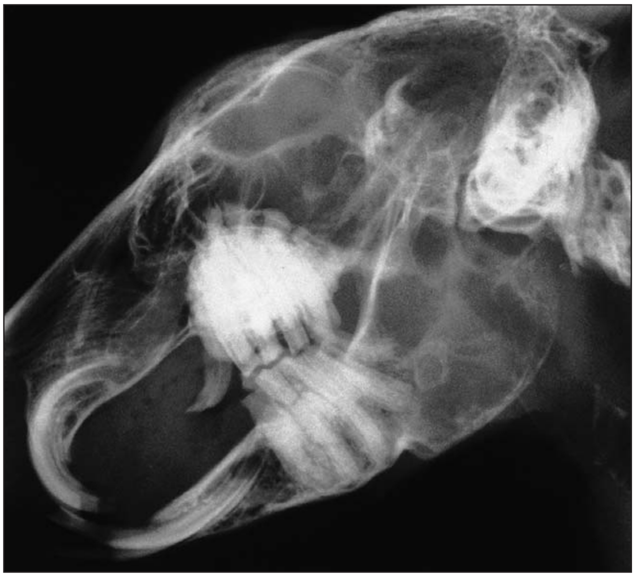


Figure 8.17 • Lateral radiograph of skull of dwarf rabbit with incisor and molar malocclusion secondary to a combination of congenital mandibular prognathism and poor diet since birth.

CLINICAL NOTE

When performing abdominal surgery, elevate the linea alba well to avoid incising the viscera underneath. The tendon is so thin that stitching the midline means stitches in the rectus abdominis muscle. On opening into the cavity, the main organs (cecum and colon) run obliquely from the right liver lobes, caudally to the left side of the bladder (Fig. 8.21).

Stomach

The stomach is 'J'-shaped, thin walled and lies on the left side. The cardia is lined by non-glandular stratified squamous epithelium. The fundus is glandular and its parietal cells secrete acid and intrinsic factor; the chief cells secrete pepsinogen. The pylorus is heavily muscled with a well-developed sphincter (Cruise & Nathan 1994). The stomach normally contains a mixture of food, fur, and fluid, even 24 hours post feeding. The pH 1–2 of the adult rabbit makes the stomach and small intestine almost sterile (Jenkins 2000)(Fig. 8.18).

CLINICAL NOTE

Gas distension after death due to autolysis often ruptures the thin stomach wall, so this is a common and normal postmortem finding. The presence of hair in the stomach is normal and due to rabbit grooming behavior. However, large hair impactions (hairballs or trichobezoars) are indicative of dehydration and lack of gastric motility (Brooks 1997; Donnelly 1997).

Neonatal stomach

The neonate stomach has a pH 5.0–6.5 (Brewer & Cruise 1994; Harkness & Wagner 1995; Jenkins 2000) and a stomach full of milk curd. This would make an ideal breeding ground for bacteria but for the fact that, in the first 3 weeks of life, it is acidified by the production of *milk oil*. This consists of octanoic and decanoic fatty acids produced by the enzymatic reaction of the suckling rabbit's digestive enzymes with the doe's milk (Harkness 1990; Harkness & Wagner 1995). Hand-reared rabbits lack this protective antimicrobial factor, making them very susceptible to infections. From about 2 weeks of age young rabbits also begin to acquire some gut flora by eating the doe's cecotrophs. By the time milk oil production ceases at 4–6 weeks some organisms will have managed to colonize the cecum to produce the hindgut fermentation. At weaning the pH drops to adult pH 1–2, which keeps the stomach relatively microbe free (Brooks 1997; Cheeke 1987a).

CLINICAL NOTE

Weaning is a critical time in the rabbit's life. The protective effect of milk oil has waned and the pH has not yet reached the adult pH 1–2. If the gut is not colonized by healthy bacteria, coliforms and clostridia can proliferate causing rapid enterotoxemia. This is easily precipitated by a low fiber, high starch diet (Brooks 1997).

Small intestine

The small intestine is relatively short and comprises only 12% of the gastrointestinal volume. This is the site of digestion and absorption of sugars and protein from food

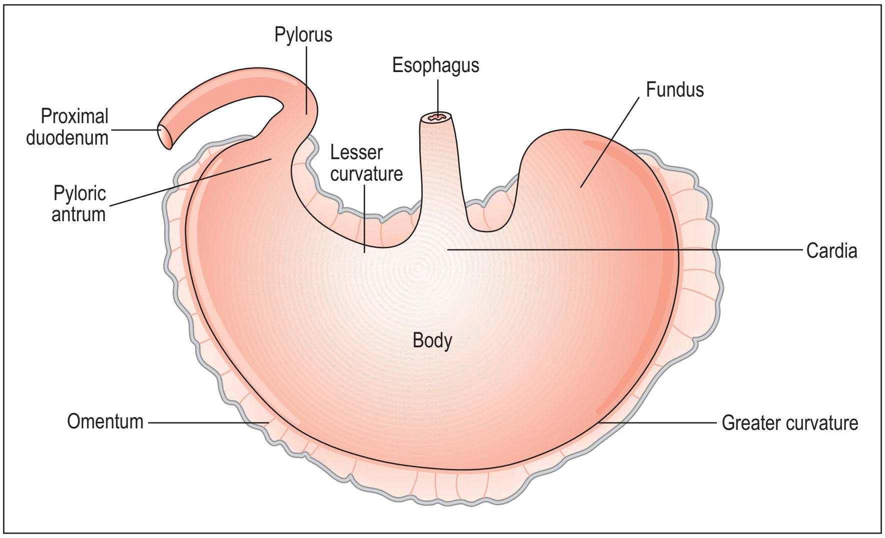


Figure 8.18 • External view of rabbit stomach showing location of cardia in the center of lesser curvature. This means that rabbits cannot vomit so need not be fasted prior to anesthesia. From Popesko, P., Rajtova, V., & Horak, J. (1990) A colour atlas of anatomy of small laboratory animals. Vol. 1. Aylesbury, UK: Wolfe with permission.

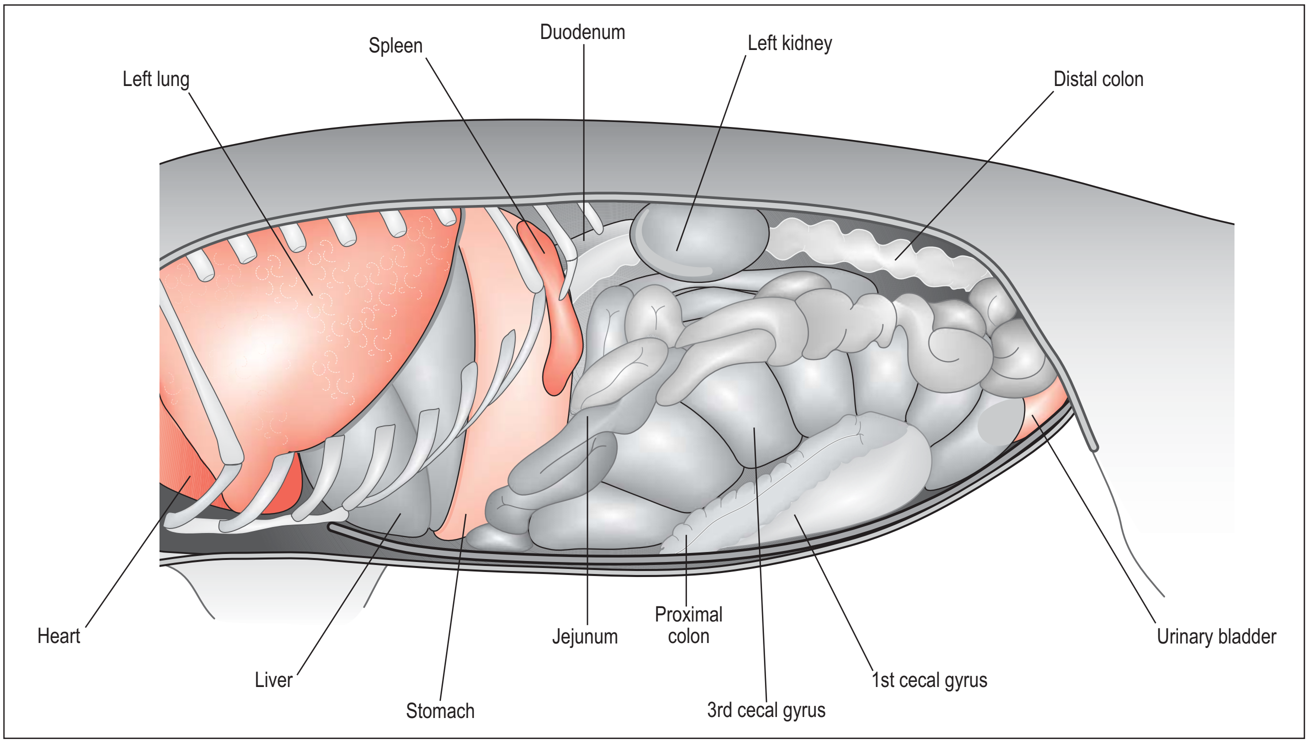


Figure 8.19 • Left lateral view of abdominal viscera (with some ribs removed). From Popesko, P., Rajtova, V., & Horak, J. (1990) A colour atlas of anatomy of small laboratory animals. Vol. 1. Aylesbury, UK: Wolfe with permission.

items, as well as of vitamins, proteins, and fatty acids from the cecotrophs (Cheeke 1987a). Moitilin is secreted by the endocrine cells of the duodenum and jejunum and helps to stimulate gastrointestinal motility in the small intestine, colon, and rectum (but not in the cecum). High carbohydrate diets inhibit its secretion and lead to gut stasis problems; fats, however, stimulate moitilin release (Brewer & Cruise 1994).

The duodenum lies at an acute angle to the liver and can be compressed by it. Unlike in most mammals, the bile duct and pancreatic duct enter the duodenum at widely separated points: the bile duct near the beginning and the pancreatic duct at the end of the duodenum (Cruise & Nathan 1994).

CLINICAL NOTE

Rabbits are unable to vomit and the duodenum becomes easily compressed by the liver. Stomach distension and life-threatening bloat can occur with hepatomegaly or if the stomach becomes impacted by hair.

The jejunum is slightly less thick and vascular than the duodenum. Aggregates of lymphoid tissue (Peyer patches) in the lamina propria become most prominent towards the ileum. The terminal ileum enlarges into a dilation called the sacculus rotundus, which is unique to the rabbit (Fig. 8.22). This lies in the left caudal abdominal quadrant and is often called the *cecal tonsil*; it has many lymph follicles that give it a honeycomb appearance. This opens into the ampulla coli at the junction between the ileum, colon, and cecum. A weak valve, the ileocecal valve, allows the chyme to pass one way into the cecum (Cruise & Nathan 1994).

Hindgut

The hindgut is well developed and consists of the cecum and colon (Figs. 8.19 and 8.20).

Cecum

The rabbit cecum is the largest of all animals, relative to size, with 10 times the capacity of the stomach and containing 40% of the intestinal content (Cruise & Nathan 1994; Jenkins 2000). It is very thin walled and coils on itself in three gyral folds before ending in a blind-ended, thick-walled tube called the vermiform appendix. The appendix is rich in lymphoid tissue and also secretes bicarbonate to buffer the cecal acids and water to form the semi-fluid cecal paste (Harkness & Wagner 1995). Unlike many other herbivores, the main cecal microorganisms in the rabbit are not lactobacillus but *Bacteroides* spp., plus ciliated protozoa, yeasts, and small numbers of *Escherichia coli* and clostridia (Cheeke 1987a; Harkness & Wagner 1995).

CLINICAL NOTE

The cecal wall is very thin and can tear easily so it is important to avoid handling, or even touching it, during surgery if at all possible.

The cecum acts like a large fermentation vat where the microbial flora break down cellulose and proteins into volatile fatty acids (VFAs) which are then directly absorbed across the cecal epithelium into the bloodstream. Its contents are semi-fluid and have an alkaline pH in the morning and acid pH in the mid afternoon. Changes in pH cause "transfaunation", which is a change in the type of microorganisms present (Brewer & Cruise 1994).

Unlike ruminants, the predominant VFA in the rabbit is acetate, regardless of diet, followed by butyrate and propionate. This is caused by the dominance of *Bacteroides* spp. instead of lactobacillus in the cecum (Carabano & Piquer 1998; Cheeke 1987d) (Table 8.1).

Cecotrophy

Coprophagy is the consumption of feces; cecotrophy refers to the consumption of cecal pellets. Cecotrophy starts between 2 and 3 weeks of age when kits start to eat solids (Carabano & Piquer 1998). They start by ingesting maternal cecotrophs first. Cecotrophy is essential for rabbit health and the lack of cecotrophy leads to a lower level of nutrients and reduced availability of protein and B and K vitamins (Eden 1940).

Cecotrophs (or night stools) are formed in the proximal colon and cecum. While the high fiber pellets (>0.5 mm in size) do not enter the cecum, but are excreted rapidly, the fine fiber particles and fluid remain in the cecum to form high nutrient particles. These become coated with mucus

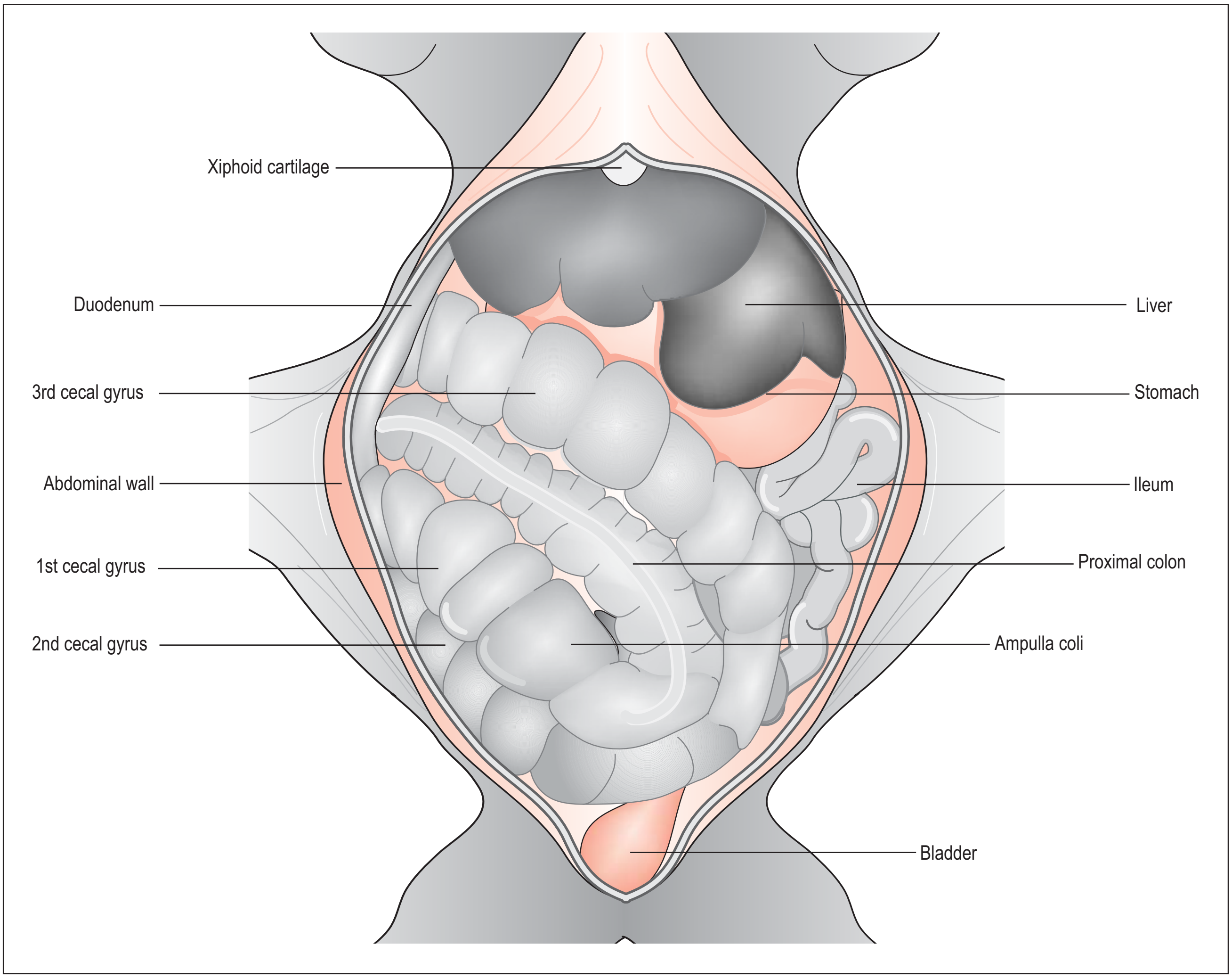


Figure 8.20 • Diagram showing ventral view of abdominal viscera.

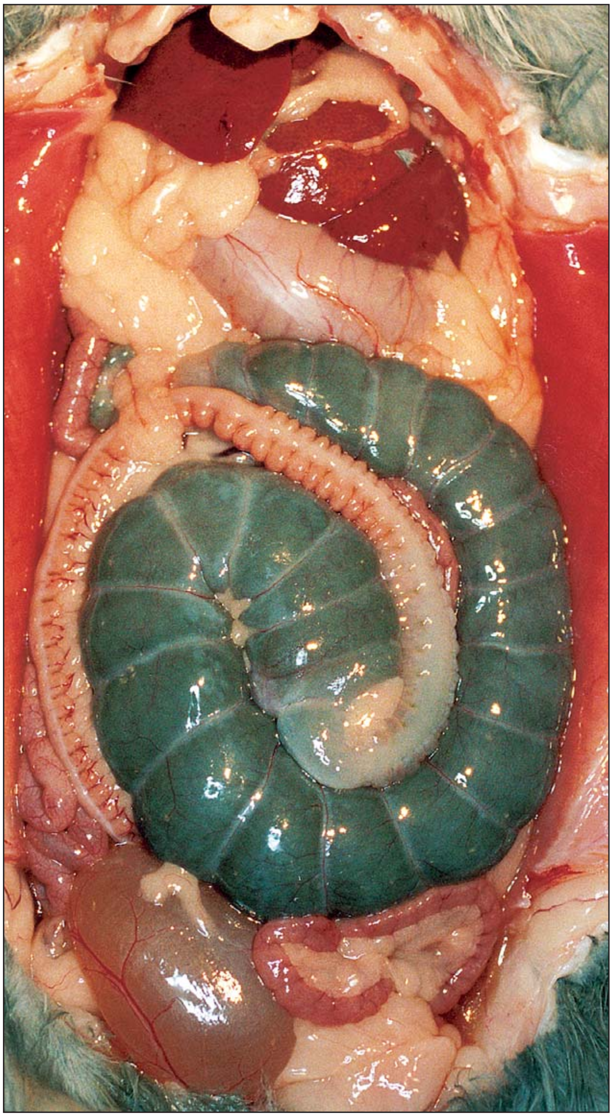


Figure 8.21 • Ventral view of abdominal viscera.

produced by the goblet cells of the colon before passing out through the anus as grape-like clusters. They are ingested directly from the anus by anal reflex and are swallowed whole without mastication. When they reach the fundus of the stomach, where further fermentation takes place over 3–6 hours, the mucus coating protects them from digestion (Cheeke 1987a).

Circadian rhythm

Although wild rabbits produce cecotrophs during the day when sleeping in their burrow, pet rabbits tend to produce hard pellets 4 hours post feeding and cecotrophs 8 hours post feeding, which tends to be at night.

Effect of diet on cecotrophy

High fiber diets are essential for cecotrophy. Low fiber diets increase cecal retention time, leading to hypomotility of the gut, and reduces the amount of cecotrophs produced. Indigestible fibers like cellulose and lignin (crude fiber digestibility of 15%) are the best way of preventing enteritis as they stimulate most hindgut motility. Non-lignified fiber like beet pulp (crude fiber digestibility of 60%) are less effective (Cheeke 1994).

A low protein diet encourages the rabbit to eat more cecotrophs in order to alleviate the deficiency whereas a diet high in protein and low in fiber reduces their consumption (Cheeke 1987b).

High carbohydrate diets produce two-fold problems. Excess glucose provides a medium for the bacteria like *Clostridium spiroforme* and *E. coli* to colonize. These diets also produce excess VFAs in the cecum, leading to a drop in pH, which in turn inhibits normal flora and allows pathogens to proliferate (Cheeke 1987g, 1994). High starch foods like maize (corn) is the least satisfactory; oats and barley are better as they are higher in fiber while being lower in starch (Cheeke 1987d, 1994).

Fats can be used as source of energy without causing cecal hyperfermentation. Full-fat soybeans and oilseeds are good sources and vegetable oil is better than animal fat (Cheeke 1994).

Colon

Although anatomically the colon has an ascending, transverse, and descending portion, functionally it is divided into a proximal part (approx. 50 cm) and a longer distal part (approx. 90 cm) (Fig. 8.22). The proximal colon has three parts: three longitudinal muscular bands called *taenia* creating three haustra (sacculations), a single taenia/haustra and the fusus coli. The distal colon has no sacculations (Carabano & Piquer 1998; Ehrlein et al. 1983; Ruckebusch & Hornicke 1997).

The fusus coli is unique to lagomorphs. It is a 5–8 cm area of thickened circular muscle lined by thick mucosa (Cruise & Nathan 1994). It is heavily supplied with ganglion cells and is under the influence of aldosterone and prostaglandins. It serves as a pacemaker, regulating the passage of ingesta into the distal colon. It controls three types of colonic motility: segmental, peristaltic, and haustral and it is these differing form of contractions which produce the hard and soft feces (Ehrlein et al. 1983; Ruckebusch & Hornicke 1997).

CLINICAL NOTE

Colonic motility and cecotrophy are regulated by the autonomic nervous system and aldosterone. This means that any kind of stress, like surgery or diet change, increases adrenaline (epinephrine), which can inhibit gastrointestinal motility and lead to cecal stasis and abnormal cecotrophs (Cheeke 1987g; Lebas et al. 1997a).

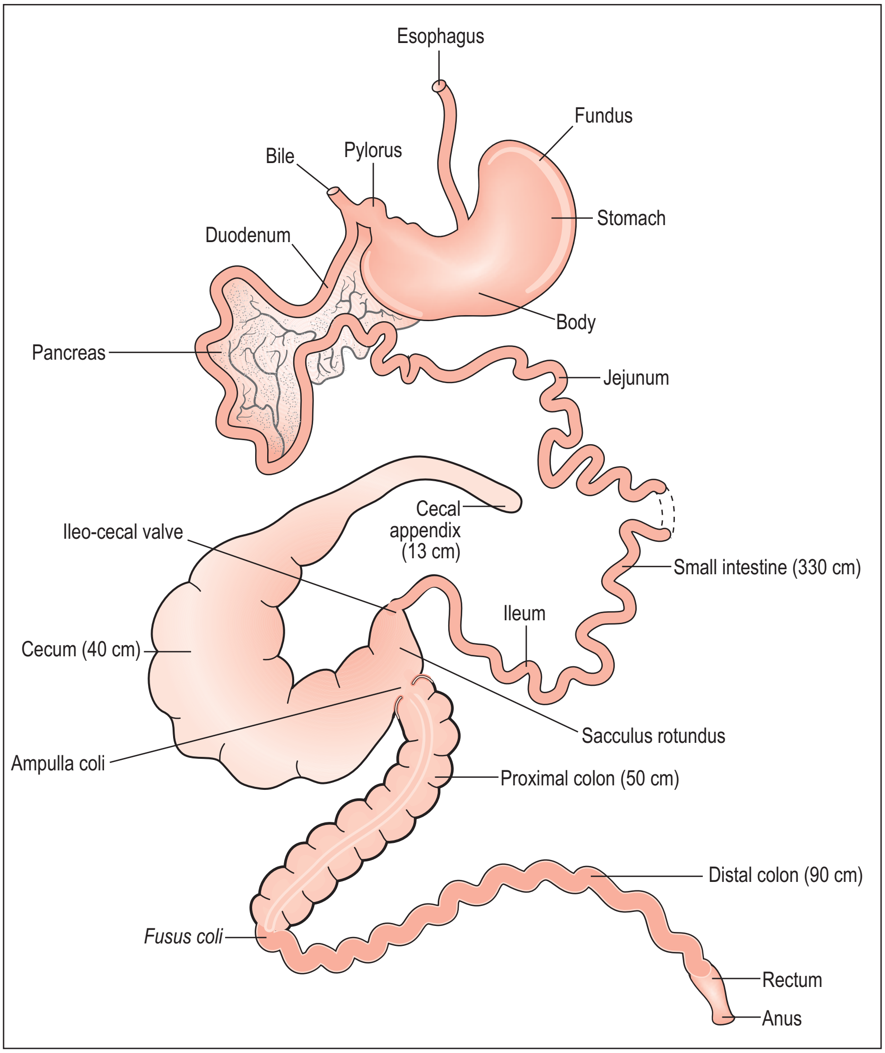

Esophagus
Fundus
Bile
Pylorus
Stomach
Duodenum
Body
Pancreas
Jejunum
Cecal appendix (13 cm)
Ileo-cecal valve
Small intestine (330 cm)
Ileum
Cecum (40 cm)
Sacculus rotundus
Ampulla coli
Proximal colon (50 cm)
Distal colon (90 cm)
Fusus coli
Rectum
Anus

Figure 8.22 • Diagram of digestive tract of the rabbit.

Production of hard feces

Segmental and haustral contractions in the proximal colon (particularly of the single haustra) mechanically separates the ingesta into solid indigestible particles and liquid contents. The large, solid pellets pass down in the middle of the lumen, further water is absorbed and they are excreted as hard dry pellets. The liquid fraction and smaller particles move to the periphery into the haustrae where they are returned by antiperistalsis into the cecum for further fermentation (Cheeke 1987a; Ehrlein et al. 1983; Ruckebusch & Hornicke 1997).

Production of soft feces (cecotrophs)

Segmental and haustral contractions are reduced and the cecum contracts to expel a soft paste into the proximal colon. Motility is decreased in the proximal colon under prostaglandin influence but enhanced in the distal colon so that the digesta passes rapidly down with no separation and no water absorption (Ehrlein et al. 1983; Ruckebusch & Hornicke 1997).

CLINICAL NOTE

Athough vomiting is not possible and diarrhea is rare in adult rabbits, decreased water and electrolyte absorption from the colon with intestinal hypomotility leads rapidly to dehydration. Consequently, fluid therapy is essential for rabbits with gastrointestinal disease (Cheeke 1987g, 1994).

KEY POINTS

- Weanling rabbits become vulnerable as the protective effect of mothers “milk oil” wanes.
- The fusus coli controls separation of hard and soft feces.
- Indigestible fiber (cellulose and lignin) is essential to drive the gut.
- High protein and high starch foods lead to gastrointestinal tract motility problems.
- High fiber and fats increase gastrointestinal tract motility.
- *Bacteroides* spp. are the main bacteria of the hindgut.
- Stress, via aldosterone, inhibits gastrointestinal motility, leading to intestinal stasis.

Liver

The liver has four lobes with a deep cleft dividing it into right and left lobes. Each lobe is then subdivided into medial and lateral. The right lobe has two further subdivisions, with the quadrate lobe in the midline and the caudate lobe near the right kidney. This small lobe has a narrow attachment to the hilar region of the liver and could be a site of liver torsion.

The gall bladder is located very deep in the right anterior lobule. The hepatic ducts unite to form the common bile duct, which receives the cystic duct from the gall bladder and enters the proximal part of the duodenum (Cruise & Nathan 1994).

Rabbits secrete about seven times as much bile as a dog of similar weight. (A 2 kg rabbit secretes 250 ml bile daily) (Brewer & Cruise 1994). They resemble birds and reptiles in that they secrete mainly biliverdin (63%) rather than bilirubin. This is due to low levels of bilirubin reductase, which reduces biliverdin to bilirubin (Cheeke 1987a; Jenkins 2000).

CLINICAL NOTE

Anorexia in rabbits can rapidly lead to fatal hepatic lipidosis. This is caused by prolonged hypoglycemia inducing lipolysis of fat stores into fatty acids. When the body cannot metabolize these excess free fatty acids they accumulate in hepatocytes of the liver, literally turning it into lard. Obese rabbits will already have some degree of fatty liver so even mild anorexia can cause life-threatening hepatic lipidosis.

Pancreas

This is a diffuse, irregular mass lying in the duodenum and is relatively small. The pancreatic duct enters the distal duodenum some 35–40 cm from the bile duct (Cruise & Nathan 1994).

URINARY SYSTEM

Water intake

Rabbits are thirsty animals. The average intake is 120 ml/kg so a 2 kg rabbit will drink as much per day as a 10 kg dog (Cheeke 1994; Harkness & Wagner 1995). The amount of water will be influenced by the ambient temperature and the composition and quantity of feed. Rabbits fed a lot of fresh greens obviously will drink less (Brewer & Cruise 1994). Dry food diets and high fiber diets increase water intake to moisten the ingesta in transit.

Rabbits will drink excessively if fasted and can drink as much as 650% of normal fluid intake on the third day of anorexia. This can result in sodium depletion (Brewer & Cruise 1994; Lebas et al. 1997a).

CLINICAL NOTE

A cardinal sign of dental disease can be polydipsia, secondary to painful teeth causing anorexia.

Kidney

The right kidney lies cranial to the left (Fig. 8.23). The rabbit kidney is quite primitive in comparison to that in other mammals. However, it has been extensively researched as its kidney tubules can be easily removed with the basement membrane intact, facilitating renal research. The kidneys are unipapillate meaning that one papilla and calyx enter the ureter (Brewer & Cruise 1994; Cruise & Nathan 1994).

A feature of the rabbit kidney is that, like neonatal mammals, not all glomeruli are active at one time. This means that a well hydrated rabbit can activate dormant glomeruli and increase diuresis without having to increase renal plasma flow and glomerular filtration rate (Brewer & Cruise 1994; Cruise & Nathan 1994).

Reabsorption of bicarbonate from the renal tubules is not as efficient as in other mammals due to the lack of carbonic anhydrase. This enzyme catalyzes the conversion of carbon

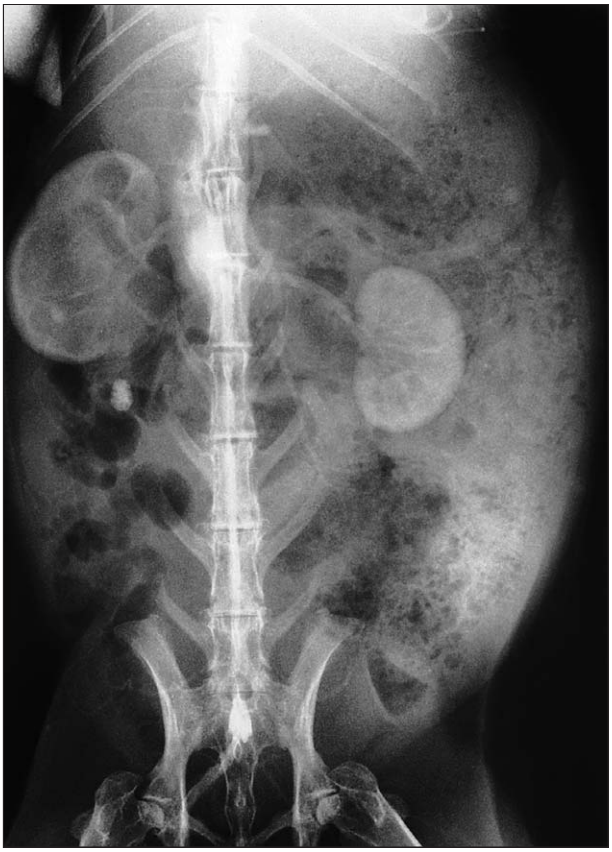


Figure 8.23 • Intravenous urogram in a 2-year-old rabbit with a long-standing ureteral calculus. A benign embryonal nephroma had caused hydronephrosis and hydroureter of the right kidney.

dioxide to bicarbonate, and vice versa, acidifying luminal fluid in the collecting ducts. As rabbits also produce high levels of bicarbonate from bacterial fermentation this means they easily get a surplus of bicarbonate and metabolic alkalosis (Brewer & Cruise 1994). Rabbits consequently excrete a much more alkaline urine than other animals like rats (Cheeke 1987e).

Rabbits are also more vulnerable to acid loads because they lack the normal mammalian renal ammonium buffering system. In most mammals metabolic acidosis (i.e., a drop in serum pH or low bicarbonate) increases the rate of ammonia, which then combines with hydrogen ions and is excreted as the buffer ammonium. This process only occurs in the rabbit in response to low bicarbonate levels making them susceptible to acid–base imbalances (Brewer & Cruise 1994; Cheeke 1987e).

Urine

Rabbits are less able to concentrate their urine and so pass copious amounts. Urine volume varies widely with environment and animal, ranging from 20–350 ml/kg per day, with an average of about 130 ml/kg (Brewer & Cruise 1994). The specific gravity is from 1.003 to 1.036 (average 1.015) and it is alkaline with a pH 7.6–8.8 (lower in a fasting rabbit). Occasional traces of protein and glucose may be present. Crystals (triple phosphate, calcium carbonate) are found in large quantities, but casts, epithelial cells, and bacteria are usually absent.

CLINICAL NOTE

Rabbit fed high calcium diets excrete nearby all the calcium via the urine. This combined with the alkaline pH can cause precipitation of solutes and urolithiasis (Fig. 8.24)

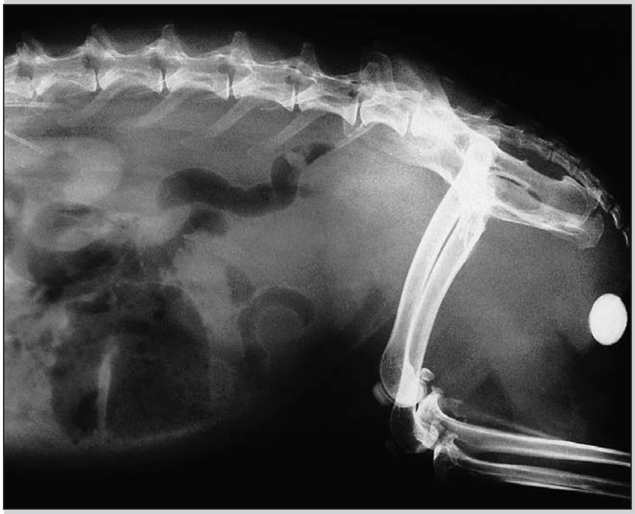


Figure 8.24 • Lateral radiograph of buck rabbit with large urolith obstructing distal urethra. Intestinal ileus is present secondary to anorexia and pain.

Urine is the major route for excretion of magnesium and calcium (Kennedy 1965). It is normally cream colored due to the high levels of calcium carbonate but it can vary from yellow to red in color. Plant pigments commonly produce a bright red urine, which can be confused with hemorrhage (Cheeke 1994).

Calcium metabolism

Calcium absorption and excretion is very different in rabbits (Cheeke 1987e; Kennedy 1965). In most mammals calcium absorption is related to the animal's needs and is regulated by the interaction of parathyroid hormone (PTH) with vitamin D3. Low calcium levels stimulate PTH to produce more Vitamin D3 in the kidney, which then acts on the gut to increase calcium absorption. It also increases tubular reabsorption of calcium from the kidneys and phosphorus excretion. The reverse happens when calcium levels are high.

Rabbits, including wild rabbits, have a much higher (30–50%) plasma calcium level than most mammals; in fact they frequently have blood plasma levels as high as that seen in laying hens (Chapin & Smith 1967a; Cheeke 1994; Kennedy 1965). Dietary calcium rapidly increases serum calcium and decreases phosphorus (Chapin & Smith 1967a). This is controlled by rapid changes in PTH, which stimulates passive absorption of calcium from the gut, independent of Vitamin D (Fairham & Harcourt-Brown 1999; Kennedy 1965).

Excretion of calcium rises during hypercalcemia and decreases with lowered serum levels. Unlike other mammals that excrete calcium via the bile, rabbits excrete calcium via the kidneys. In contrast to rats, which have been shown to excrete 2% of dietary calcium in their urine, rabbits can excrete up to 60% of that ingested (Cheeke & Amber 1973). Phosphorus, however, is excreted through the feces. The rabbit kidney has a fractional excretion of calcium of 44.9% compared to 2% in most mammals. In fact a 2–3 kg rabbit would excrete as much calcium as an adult human. This is facilitated by a high level of plasma calcium combined with a low rate of tubular reabsorption (Buss & Bordeau 1984; Kennedy 1965).

The Ca:P ratio is not as critical in rabbits as in other species as they are extremely tolerant of high calcium intakes. In most vertebrates the ratio is usually about 2:1, but it has been found that growing rabbits are not adversely affected by diets as high in calcium as 12:1 (Chapin & Smith 1967a).

CLINICAL NOTE

Although rabbits are extremely tolerant of high calcium levels, high levels of phosphorus could adversely affect bone calcification and growth, so if a diet contains excess amounts of phosphorus, like wheat bran, a calcium supplement may be needed (Chapin & Smith 1967b).

Vitamin D

The role of vitamin D in rabbits is still not fully evaluated as even a three- to four-fold increase in Vitamin D has no effect on serum calcium. Calcium levels are controlled instead by renal homeostasis. A diet low in calcium was found to decrease calcium excretion and increase phosphorus under the influence of elevated PTH levels in young growing rabbits (Bordeau et al. 1988).

However, chronic deficiency of Vitamin D does lead to mild hypocalcemia, elevated PTH and reduced excretion of both calcium and phosphorus. It is thought that although Vitamin D plays little role in passive intestinal absorption with normal dietary calcium levels it does increase calcium absorption by active transport when dietary calcium levels are low. Vitamin D also regulates phosphorous metabolism, leading to severe hypophosphatemia if deficient (Bordeau & Schwer-Dymerski 1986).

Oversupplementation with calcium or Vitamin D could lead to metastatic calcification of soft tissues like the aorta and kidneys (Cheeke 1987e). As the kidney controls calcium levels, renal damage could also impair excretion and cause hypercalcemia and metastatic calcification.

CLINICAL NOTE

Rabbit urine is normally cream colored due to the excess calcium being excreted in the urine. Growing kits, pregnant does or malnourished rabbits may have clear urine due to increased calcium retention.

KEY POINTS

- Unlike most mammals the main route of calcium excretion is through the urine.
- Rabbits naturally have high serum calcium levels, which is in direct proportion to dietary calcium levels.
- Efficient calcium absorption from the diet is independent of Vitamin D.
- Rabbits have a much higher fractional excretion of calcium than other mammals.

REPRODUCTIVE SYSTEM

Male

The male has a rounded penile sheath with a round urethra. They can be easily extruded in rabbits over 2-months-old. On either side of the anogenital area are blind, hairless inguinal sacs, which contain scent glands. The testes descend at 10 weeks and the hairless scrotal sacs can be seen cranial to the penis. They are relatively large with large epididymal fat pads. There is no os penis (Donnelly 1997).

Accessory glands

The seminal vesicles open into the prostatic section of the urethra. The small paired bulbourethral glands form a bilobed swelling in the dorsal wall of the urethra, just behind the prostate (Cruise & Nathan 1994).

Female

The ovaries are elongated and located more caudally than in cats and dogs. The oviducts are very long and coiled. The uterus is duplex, being separate along its length and forming two cervices, uniting only to form a long vagina (Figs. 8.25 and 8.26).

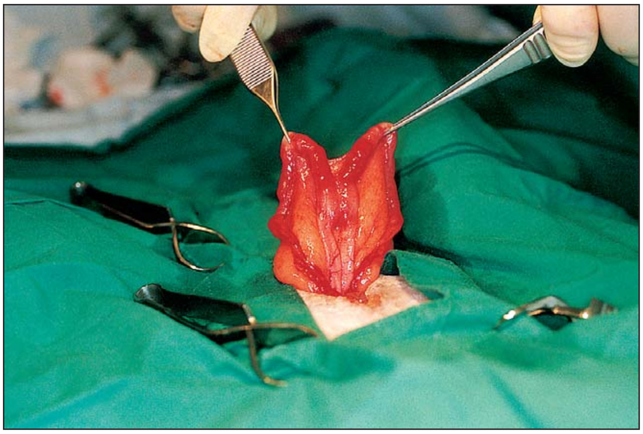


Figure 8.25 • Rabbit ovariohysterectomy showing duplex uterus – there are two cervices and a large saccular vagina. The mesometrium is a site of fat storage so early spaying is advised.

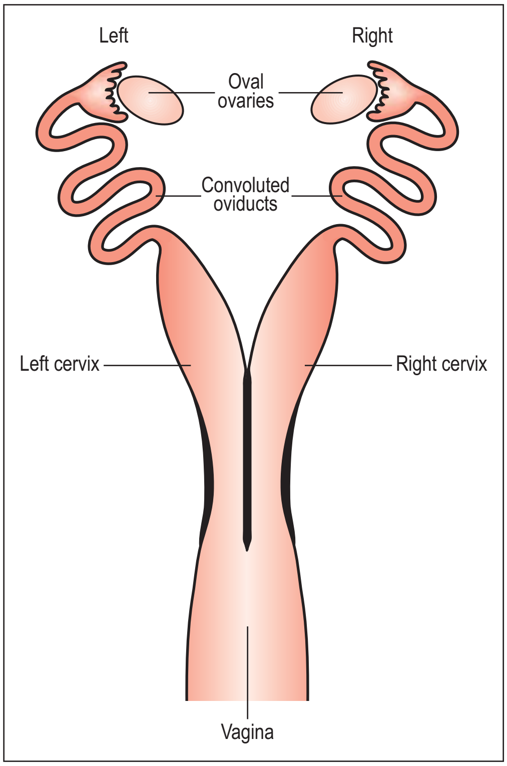


Figure 8.26 • Duplex uterus of the rabbit.

It is colored bright pink and lies dorsal to the urinary bladder. The mesometrium is a site of fat storage and, even in young does, builds up fat tissue rapidly. The suspensory ligaments are long, making exteriorization of the uterus easy. The urethra enters the vagina via the vestibule, in the dorsal wall of which is found the bulbourethral gland, while the clitoris lies along the ventral surface (Cruise & Nathan 1994). The rabbit has only a minor anastomoses between the uterine and ovarian vasculature, unlike the guinea pig and rat where the arteries and veins share many common associations (Del Campo & Ginther 1972).

CLINICAL NOTE

The uterus and ovarian pedicle are more friable than in the cat or dog so early spaying (before 6 months) is advisable to avoid excess fat.

Reproductive physiology

Rabbits literally do "breed like rabbits." In fact the cult of the Easter Bunny arose from the old pagan spring festival symbolizing new life and fertility. Smaller breeds reach sexual maturity at 4–4.5 months while large breeds mature at 4.5–5 months (Batchelor 1999). The reproductive capacity of rabbits is potentially up to 60 young per year as the doe has a post partum estrus within 24 hours of kindling (Lebas et al. 1997b).

Ovulation

Rabbits, just like the cat and ferret, are induced ovulators (Bell 1999) and ovulation occurs 10 to 13 hours after coitus. There is no regular estrous cycle but a period of receptivity every 5 to 6 days. Ovarian activity decreases with shorter days in late summer to winter.

The vaginal smear technique is not useful in the rabbit but the appearance of the vulva can give a guideline. Anestrus shows a narrow, pale pink vulva, while during estrus the vulva becomes swollen and reddish purple under the effect of estrogen (Batchelor 1999; Lebas et al. 1997b).

Pregnancy

The gestation period is 31–32 days. Larger litters have shorter gestation periods than small litters. A fetus can be felt by gentle palpation between 12 and 14 days gestation. If a litter has not kindled by day 32 there is a higher risk of the kits being stillborn.

Embryonic mortality is very high in rabbits with only about 60 to 70% successful births (Lebas et al. 1997b). Rabbits are particularly prone to fetal loss at day 13, when placentation changes from yolk sacs to hemochorial, and at 23 days when the fetuses are susceptible to dislodgement by rough handling (Harkness & Wagner 1995). External factors like poor nutrition or body condition, age, and time of year also play a role (Lebas et al. 1997b).

Parturition

Within the last week of kindling estrogen increases as progesterone declines, causing hair loss to line the nest. Oxytocin peaks prior to parturition. Parturition usually occurs in the early morning and normally takes about 30 minutes, although young have been born hours or even days apart.

Neonates

The young are altricial with sealed eyelids and ear canals and weigh 40–50 g (Harkness & Wagner 1995; Nowak 1999b). Like the guinea pig and humans, rabbits get their passive immunity before birth (Brewer & Cruise 1994). Neonates are very vulnerable to hypothermia as they are hairless and the doe shows little maternal behavior. They keep warm via brown fat, which is highest in the first 2 weeks and helps protect against low ambient temperatures. Rabbit pups are normoglycemic, even without suckling until 6 hours post partum when the glycogen reserves become exhausted (Brewer & Cruise 1994; Harkness & Wagner 1995).

Pseudopregnancy

Pseudopregnancy can be caused by infertile mating or the presence of a male nearby. It can last for 16 or 17 days during which the dam will be unable to conceive. After 18 to 22 days she may pluck hair from her belly to make a nest. During pseudopregnancy the corpus luteum secretes progesterone, which causes the uterus and mammary glands to grow. This is most pronounced in the first 10 days; by day 16 the organs will involute and at day 18 the corpus luteum will be disintegrating (Lebas et al. 1997b).

Lactation

The eight mammary glands develop in the last week of pregnancy. Milk let down will be delayed until after kindling. There is a post partum estrus but receptivity declines once lactation begins and continues until after weaning.

Rabbit milk is richer than cow milk, with an unusually low lactose content and very high protein and fat content (13% protein, 9% fat, 1% lactose, 2.3% minerals) (Cheeke 1987d, 1987h). Suckling is stimulated via a pheromone produced by a gland near the nipple. Consumption of water increases 10-fold during lactation, as does consumption of cecotrophs.

CLINICAL NOTE

Many rabbit owners think the doe has abandoned her young. However, the doe only nurses her young once a day, spending about 3–5 minutes with them. Her milk is so rich the kits can ingest 20% of body weight while suckling (Cheeke 1987h; Lebas et al. 1997b).

ENDOCRINE SYSTEM – ADRENALS

The adrenal glands are located craniomedial to the kidneys and lie flattened against the dorsal body wall. The left lies caudolateral to the cranial mesenteric artery and the right lies in close proximity to the caudal vena cava (Cruise & Nathan 1994). Cecotrophy is under the control of the adrenals, which is why stress can lead to severe secondary digestive problems.

SENSES

Being a prey species, the rabbit has acutely developed sense organs. Like rodents, rabbits have acute hearing and are very sensitive to high frequency sounds (Batchelor 1999). The ears are long and funnel shaped to gather sound, and the eyes are laterally located, offering binocular vision.

Eyes

The orbits are laterally situated with prominent globes and the rabbit can obtain almost 360 degree vision by tilting the head and moving the eyes. The upper lid is shorter and thicker than the lower lid with more numerous cilia. Rabbits blink only 10 to 12 times per hour, which makes them predisposed to corneal ulceration and dry eye and they have been used – and abused – as models for opthalmological research (Andrew 2002; Peiffer et al. 1994). The third eyelid does not visibly nictitate but can be retracted by applying pressure to the globe. It does not move by more than two-thirds across the globe (Peiffer et al. 1994).

The orbit is circular and made of bone, except at the lower rim where it is walled by the muscles of mastication. The rabbit has one more extraocular muscle than most mammals, making a total of nine. This is because the globe extends beyond the lower rim so the depressor palpebrae muscle is necessary to depress the lower lid (Peiffer et al. 1994).

Blood supply

The internal maxillary artery enters the orbit where it gives rise to the external ophthalmic artery. This anastomoses with the internal to supply the extraocular muscles. An extensive postorbital venous sinus provides venous drainage and must be avoided if operating to enucleate the eye (Peiffer et al. 1994).

Lacrimal system

The aqueous tear film is produced by three glands which empty via the lacrimal puncta and canaliculi into the nasolacrimal duct. Normal Schirmer tear tests are 5 (2.96) mm/minute (Peiffer et al. 1994).

The lacrimal gland

The lacrimal gland is large, bilobed, pale red in color and lies beside the lower rim with a bulbous enlargement at the medial canthus. It plays a lesser role in tear secretion so portions can be removed without adverse long-term effects to tear production (Peiffer et al. 1994).

Harderian gland

This is also called the “deep gland of the third eyelid” and is attached to the rostromedial wall of the orbit. The gland is large, encapsulated, and measures about 15×5 mm. It is surrounded by the orbital venous sinus. It is kidney shaped and has two distinct lobes. The excretory ducts from both lobes converge into one duct which opens behind the third eyelid. The gland is larger in males than females and is at its largest during the breeding season (Peiffer et al. 1994).

Third eyelid gland

This is also called the “superficial gland of the third eyelid.” This gland is similar to the Harderian gland and surrounds the shaft of the third eyelid.

Nasolacrimal duct

The rabbit is unique in having only one lacrimal puncta located on the lower eyelid 3 mm from the eyelid margins and medial canthus. A short canaliculus (2 mm) leads into the funnel shaped lacrimal sac. The duct then passes through the lacrimal bone on the medial orbit and along the maxilla where it is encased in bone. It can be divided roughly into four portions (Burling et al. 1991; Peiffer et al. 1994):

1. Nasal puncta to proximal maxillary curve where it narrows (1 mm)
2. Tubular portion along lacrimal canal to base of incisor root (2 mm)
3. ‘S’-shaped bend around incisor root (1 mm)
4. Rostral duct running through nasal cartilage to exit at tiny nasopunctum just caudal to the mucocutaneous junction

Along its length the duct is lined by a highly folded epithelium with a rich vascular and lymphatic supply. This undulating epithelium, along with the narrow, sharp bends and small nasal opening, means it can easily accumulate inflammatory debris that cause obstruction of the tear duct (Burling et al. 1991).

CLINICAL NOTE

The tortuous and narrow nasolacrimal duct with two sigmoid curves means that pet rabbits are very vulnerable to duct obstruction and dacryocystitis. Treatment can only be helped by flushing the duct and treating any underlying dental disease (Burling et al. 1991; Harcourt-Brown 1997).

Globe

The cornea is large and occupies 30% of the globe (Andrew 2002; Donnelly 1997). The rabbit pupil is ovoid vertically but becomes circular when widely dilated. The lens is large and has a poorly developed ciliary body, giving the rabbit poor accommodation. The rabbit retinal vascular pattern is merangiotic, which is characterized by a limited area of blood vessels. Albino rabbits have a non-pigmented retina. The optic nerve is located above the midline so retinal examination involves looking up into the eye. There is no tapetum lucidum and rabbits, like dogs, have a depression in the optic disk (Andrew 2002; Peiffer et al. 1994).

INTEGUMENT

Rabbits have three types of hair – long and short guard hairs and the undercoat – and it is these different lengths and types that have produced the wide variety of rabbit breeds. The primary hair follicles produce the longer guard hairs or bristles and also have a sebaceous gland and erector pili muscle attached. This enables the guard hairs to "stand on end" when the animal is cold, trapping a layer of warm air for insulation. The short guard hairs or awns are produced by lateral primary follicles; secondary follicles produce the down hairs or undercoat (Cheeke 1987h).

Rex breeds are derived from a mutation first observed in France in 1919. They have short, inconspicuous guard hairs that create fur of uniform length. The satin mutation occurred in America in the mid-1930s. The coat length is similar in this breed but the scales of the hair are smooth, creating a sheen appearance. Angora breeds have both long guard hairs and undercoat, with the females having longer hair than the males (Cheeke 1987h).

Secondary follicles can vary with the season, thickening the undercoat in rabbits from cold areas. In some wild rabbits, under the action of melatonin, the pineal gland produces a winter white coat for camouflage against the snow. Photoperiod and prolactin are the triggers for this coat change (Cheeke 1987h).

CLINICAL NOTE

The superficial fascia has a high elastic and collagen content, which means that subcutaneous injections in the scruff are much easier than in rats and guinea pigs (Cruise & Nathan 1994).

Coat color

The original pet rabbits had the natural camouflage agouti coloration and the first color variants seem to have appeared only about the middle of the 16th century. The *Madonna with the Rabbit* was painted by Titian in 1550 and featured a white rabbit; by 1700 seven mutant colors were known. The hair pigments are melanin (brown/black) and pheomelanin (red/yellow). These pigments are made from the amino acid tyrosine under the influence of the enzyme tyrosinase, which needs copper and iron as cofactors. White hair is created by lack of pigment and reflection of light (Cheeke 1987h). The sheen will depend on sebaceous gland secretions, which is influenced by the level of fat in the diet.

Himalayan rabbits grow coat color based on environmental temperature. The Himalayan gene restricts coat pigment to the extremities like the ears, nose, feet, and tail where the temperature is lower (Cheeke 1987h). Similarly, shaving hair drops the temperature and encourages the growth of pigmented hair after surgery.

Molting

Rabbits molt when the new hair forces out the old hair from the hair follicle, and this occurs twice a year in Spring and Autumn. Molting starts at the head and proceeds downward to the rear and belly, creating an unkempt moth-eaten appearance over the rump.

Feet

Rabbits have no footpads but have coarse fur on the palmar and plantar surfaces of the feet. As rabbit skin is thin, this predisposes them to pressure sores if kept on hard flooring or in unhygienic conditions. The metatarsus is particularly vulnerable as rabbits sit plantigrade, so hard surfaces can erode the fur and skin leading to ulcerative pododermatitis. This is common in Rex breeds with less coarse hair to protect the thin skin (Fig. 8.27).

Scent glands

Both sexes have three sets of scent glands, which are used for territorial and sexual marking (Donnelly 1997). They are used mostly by males and dominant females. The chin (submental) gland is used for chin rubbing against objects. There are also anal glands and inguinal glands located in the hairless area on either side of the anogenital region. These glands are influenced by androgen and produce a mixture of hydrocarbons, proteins, fatty acids, and triglycerides.

KEY POINTS

- The uterus is duplex, meaning there are two cervices leading into the vagina.
- The rabbit has only one lacrimal puncta situated on each lower lid.
- The two kinks in the duct make it difficult to cannulate and predispose it to infection.
- Incisor and molar tooth root problems can precipitate dacryocystitis.

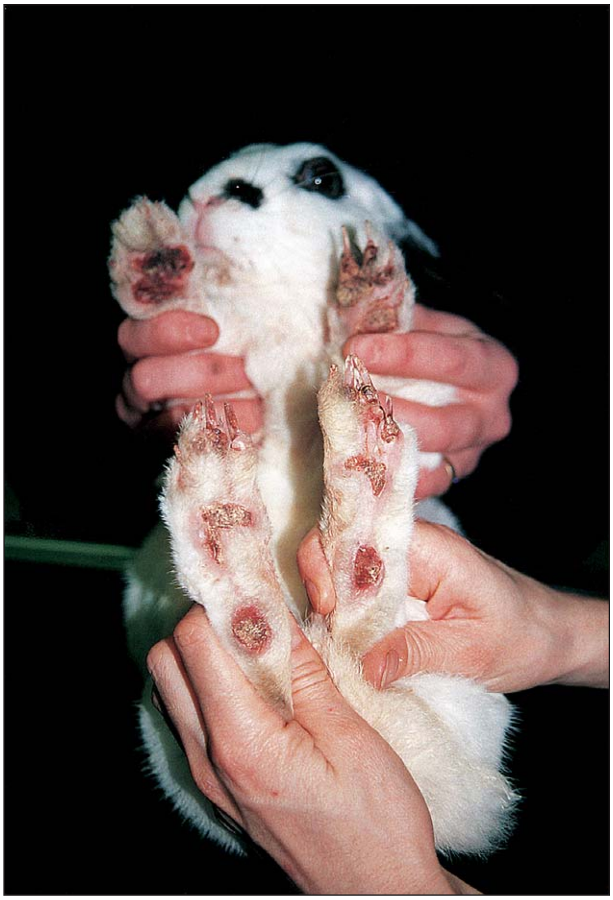


Figure 8.27 • A rabbit with severe ulcerative pododermatitis on all four feet secondary to severe urine scalding and neglect. This rabbit was found dumped in a filthy hutch in the back of a skip.

REFERENCES

Andrew, S. A. (2002) Corneal diseases of rabbits. In N. J. Millichamp (ed.), *The Veterinary Clinics of North America, Exotic Animal Practice: Opthalmology*. Philadelphia: WB Saunders. pp. 341–357.

Batchelor, G. R. (1999) The laboratory rabbit. In T. Poole (ed.), *UFAW Handbook on the care and management of laboratory animals*, 7th edn. Vol. 1. Oxford: Blackwell Science. pp. 395–409.

Bell, D. J. (1999) The European wild rabbit. In T. Poole (ed.), *UFAW Handbook on the care and management of laboratory animals*, 7th edn. Vol. 1. Oxford: Blackwell Science. pp. 389–395.

Benson, K. G., & Paul-Murphy, J. (1999) Clinical pathology of the domestic rabbit: Acquisition and interpretation of samples. In D. R. Reavill (ed.), *Clinical pathology and sample collection, The Veterinary Clinics of North America, Exotic Animal Practice*, Vol. 2. Philadelphia: WB Saunders. pp. 539–553.

Bordeau, J. E., Schwer-Dymerski, D. A., Stern, P. H., & Langman, C. B. (1986) Calcium and phosphorous metabolism in chronically vitamin D deficient laboratory rabbits. *Mineral and Electrolyte Metabolism 12*, 176–185.

Bordeau, J. E., Bouillon, R., Zikos, D., & Langman, C. B. (1988) Renal responses to calcium deprivation in young rabbits. *Mineral and Electrolyte Metabolism 14*, 150–157.

Brewer, N. R., & Cruise, L. J. (1994) Physiology. In P. J Manning, D. H. Ringler & C. E. Newcomer (eds.), *The biology of the laboratory rabbit*, 2nd edn. London: Academic Press. pp. 63–70.

Brooks, D. (1997) Nutrition and gastrointestinal physiology. In E. V. Hillyer & K. Quesenberry (eds.), *Ferrets, rabbits and rodents: Clinical medicine and surgery*. Philadelphia: WB Saunders. pp. 169–175.

Burling, K., Murphy, C. J., de Silva Curiel, J., Koblik, P., & Bellhorn, R. W. (1991) Anatomy of the rabbit nasolacrimal duct and its clinical implications. *Progress in Veterinary Comparative Opthalmology 1*, 33–40.

Buss, S. L., & Bordeau, J. E. (1984) Calcium Balance in laboratory rabbits. *Mineral Electrolytes Metabolism 10*, 127–132.

Carabano, R., & Piquer, J. (1998) The Digestive system of the rabbit. In C. de Blas & J. Wiseman (eds.), *The nutrition of the rabbit*. Oxford: CABI Publishing. pp. 1–17.

Carpenter, J. A. (1956) Species differences in taste preferences. *Journal of Comparative Physiology and Psychology 49*, 139–143.

Chapin, R. E., & Smith, S. E. (1967a) The calcium tolerance of growing rabbits. *Cornell Veterinarian 57*, 480–491.

Chapin, R. E., & Smith, S. E. (1967b) High phosphorous diets fed to growing rabbits. *Cornell Veterinarian 57*, 492–500.

Cheeke, P. R. (1987a) Digestive physiology. In T. J. Cunha (ed.), *Rabbit feeding and nutrition*. Orlando: Academic Press. pp. 15–34.

Cheeke, P. R. (1987b) Protein and amino acid nutrition. In T. J. Cunha (ed.), *Rabbit feeding and nutrition*. Orlando: Academic Press. pp. 34–60.

Cheeke, P. R. (1987c) Energy metabolism and requirements. In T. J. Cunha (ed.), *Rabbit feeding and nutrition*. Orlando: Academic Press. pp. 63–75.

Cheeke, P. R. (1987d) Carbohydrates and fibre. In T. J. Cunha (ed.), *Rabbit feeding and nutrition*. Orlando: Academic Press. pp. 77–93.

Cheeke, P. R. (1987e) Mineral nutrition of rabbits. In T. J. Cunha (ed.), *Rabbit feeding and nutrition*. Orlando: Academic Press. pp. 106–132.

Cheeke, P. R. (1987f) Feeding behaviour and regulation of feed intake. In T. J. Cunha (ed.), *Rabbit feeding and nutrition*. Orlando: Academic Press. pp. 160–173.

Cheeke, P. R. (1987g) Nutrition–disease interrelationships. In T. J. Cunha (ed.), *Rabbit feeding and nutrition*. Orlando: Academic Press. pp. 176–197.

Cheeke, P. R. (1987h) Feeding rabbits for various productive functions. In T. J. Cunha (ed.), *Rabbit feeding and nutrition*. Orlando: Academic Press. pp. 302–326.

Cheeke, P. R. (1994) Nutrition and nutritional diseases. In P. J. Manning, D. H. Ringler & C. E. Newcomer (eds.), *The biology of the laboratory rabbit*, 2nd edn. London: Academic Press. pp. 321–331.

Cheeke, P. R., & Amber, J. W. (1973) Comparative calcium excretion by rats and rabbits. *Journal of Animal Science 37*, 450–454.

Crossley, D. A. (2003) Oral biology and disorders of lagomorphs. *Veterinary Clinics of North America Exotic Animal Practice* 6(3), 629–659.

Cruise, J. L., & Nathan, R. B. (1994) Anatomy. In P. J Manning, D. H. Ringler & C. E. Newcomer (eds.), *The biology of the laboratory rabbit*, 2nd edn. London: Academic Press. pp. 47–61.

Del Campo, C. H., & Ginther, O. J. (1972) Vascular anatomy of the uterus and ovaries and the unilateral luteolytic effect of the uterus: Guinea pigs, rats, hamsters and rabbits. *American Journal of Veterinary Research 33*, 2561–2578.

Donnelly, T. M. (1997) Basic anatomy, physiology and husbandry. In E. V. Hillyer & K. Quesenberry (eds.), *Ferrets, rabbits and rodents: Clinical medicine and surgery*. Philadelphia: WB Saunders. pp. 147–159.

Eden, A. (1940) Coprophagy in the rabbit. *Nature 145*, 36–37.

Ehrlein, H. J., Reich, H., & Schwinger, M. (1983) Colonic motility and transit of digesta during hard and soft faeces formation in rabbits. *Journal of Physiology (Lond) 338*, 75–86.

Fairham, J., & Harcourt-Brown, F. M. (1999) Preliminary investigation of the vitamin D status of pet rabbits. *Veterinary Record 145*, 452–454.

Harcourt-Brown, F. M. (1996) Calcium deficiency, diet and dental disease in pet rabbits. *Veterinary Record 139*, 567–571.

Harcourt-Brown, F. M. (1997) Diagnosis, treatment and prognosis of dental disease in pet rabbits. *In Practice 19*, 407–421.

Harkness, J. E. (1990) Nutrition of rabbits and rodents. In *Rabbits and rodents laboratory animal science, University of Sydney Proceedings 142*. Sydney, NSW: University of Sydney. pp. 99–111.

Harkness, J. E., & Wagner, J. E. (1995) Biology and husbandry – the rabbit. *The biology and medicine of rabbits and rodents*, 4th edn. Baltimore: William & Wilkins. pp. 13–30.

Hornicke, H., & Batsch, F. (1977) Caecotrophy in rabbits – a circadian function. *Journal of Mammology 58*, 240–242.

Jelenko, C., Anderson, A. P., Scott, T. H., & Wheeler, M. L. (1971) Organ weights and water composition of the New Zealand Albino rabbit (*Oryctolagus cuniculus*). *American Journal of Veterinary Research 32*(10), 1637–1639.

Jenkins, J. R. (2000) Rabbit and ferret liver and gastrointestinal testing. In A. M. Fudge (ed.), *Laboratory medicine: Avian and exotic pets*. Philadelphia: WB Saunders. pp. 291–305.

Kennedy, A. (1965) The urinary excretion of calcium by normal rabbits. *Journal of Comparative Pathology 75*, 69–74.

Lebas, F., Coudert, P., de Rochambeau, H., & Thébault, R. G. (1997a) *The rabbit: Husbandry, health and production*. Vol. 2, Nutrition and feeding. Rome: FAO United Nations. pp. 19–36.

Lebas, F., Coudert, P., de Rochambeau, H., & Thébault, R. G. (1997b) *The rabbit: Husbandry, health and production*. Vol. 3, Reproduction. Rome: FAO United Nations. pp. 45–55.

Nowak, R. M. (ed.) (1999a) *Walker's Mammals of the world*, 6th edn. Vol. 11. Baltimore: John Hopkins University Express. Order Lagomorpha; pp. 1715–1721.

Nowak, R. M. (ed.) (1999b) *Walker's Mammals of the world*, 6th edn. Vol. 11. Baltimore: John Hopkins University Express. Lagomorpha; Leporidae; pp. 1729–1731.

Okerman, L. (1994) Anatomical peculiarities. In *Diseases of domestic rabbits*, 2nd edn. Oxford: Blackwell Science. pp. 10–14.

Peiffer, R. L., Pohm-Thorsen, L., & Corcoran, K. (1994) Models in ophthalmology and vision research. In P. J Manning, D. H. Ringler & C. E. Newcomer (eds.), *The biology of the laboratory rabbit*, 2nd edn. London: Academic Press. pp. 410–430.

Percy, D. H., & Barthold, S.W. (2001) Rabbit: Pathology of laboratory rodents and rabbits, 2nd edn. Ames: Iowa State University Press. pp. 248–307.

Popesko, P., Rajtova, V., & Horak, J. (1990) *A colour atlas of anatomy of small laboratory animals*. Vol. 1. Aylesbury, UK: Wolfe. Rabbit and guinea pig; pp. 11–147.

Ruckebusch, Y., & Hornicke, H. (1977) Motility of the rabbits colon and caecotrophy. *Physiology and Behavior 18*, 871– 878.

Sandford, J. C. (1996) *The domestic rabbit*, 5th edn. Oxford: Blackwell Science. History and aspects of the rabbit; pp. 1–14.

Stein, S., & Walshaw, S. (1996) Rabbits. In K. Laber-Laird, M. M. Swindle & P. Flecknell (eds.), *Handbook of rodent and rabbit medicine*. Oxford: Pergamon. pp. 183–217.

Vaughan, T. A. (ed.) (1986) *Mammology*, 3rd edn. Philadelphia: Saunders College. Order Lagomorpha; pp. 277–283.

Whitehouse, R. H., & Grove, A. J. (1968) Dissection of the rabbit. London: University Tutorial Press.

9

Guinea pigs

INTRODUCTION

The name *guinea pig* has become synonymous with the term “experimental subject” in medical research. This is because the guinea pig was the first animal to be used in research: in an experiment on heat production in 1780 (Wagner 1976).

The wild ancestor of the guinea pig, *Cavia porcellus*, comes from South America where they lived in small groups in grassland areas (Harkness & Wagner 1995). *Cavia porcellus* no longer exists in the wild and was domesticated for centuries by the Incas for religious and food purposes (Nowak 1999). The early conquistadors invading Peru from 1532 called them Indian pigs because, at the time, South America was thought to be part of the West Indies and their squeals resembled that of pigs. The origin of the word “guinea” is lost in history. Theories range from claims that they cost one guinea when first imported as pets to 16th-century England or that they came via the Dutch colony of Guyana and the name later became corrupted (Wagner 1976; Weir 1974).

The word cavy is the correct term as it derives from the South American Quechuan (vernacular). Although that is also the scientific name, the name guinea pig is still more commonly used today.

Although the guinea pig has much in common with rats and mice from a morphological perspective, recent genetic research has indicated that the caviomorphs may have evolved separately. Examination of mitochondrial DNA has shown that they may be more closely related to man, rabbits, horses, seals, and cows than to rats and mice (D’Erchia et al. 1996; Harkness & Wagner 1995).

THERMOREGULATION

Due to its compact nature the guinea pig conserves heat well but dissipates it poorly, so high temperatures lead to heat prostration and death. This is especially a problem in heavily pregnant sows. Ambient temperature ranges from 18 to 26º C are best.

GENERAL EXTERNAL ANATOMY

The guinea pig is short and squat, having a short neck merging with the main trunk (Fig. 9.1). The hind legs are longer than the front legs and there is no tail. It reaches maximum weight and length at about 15 months of age. The male is larger than the female, being 900–1200 g in comparison to the female’s 700–900 g.

The nostrils are longitudinal slits and are divided by the hairless philtrum. The mouth is triangular with the apex formed by the split upper lip. Caudal to the upper and lower incisors are skin folds that roll inwards to the midline to prevent food passing into the pharynx while gnawing. The pinna is erect in juveniles and folded forward in older adults. It is covered by fine hairs on both the medial and lateral aspects.

Unlike rats and hamsters, the guinea pig has only four toes on the front feet (digit 1 is absent) and no ability to grasp food. The hind feet are plantigrade, with only three toes (digits 1 and 5 absent), allowing less speed than the rabbit. The soles are hairless with well-defined footpads. The forefoot has a three lobed palmar pad with a caudal carpal pad; the hind foot has a bilobed plantar pad with a large tarsal pad (Cooper & Schiller 1975a)(Figs. 9.2 and 9.3).

External genitalia

Mammary glands are present in both male and female. There is a single pair in the inguinal region with two teats surrounded by a hairless area.

Male

The male has lateral scrotal swellings on each side of the anus. The cranial orifice is the penile urethra, which is covered by preputial folds. Caudally, is a longitudinal cleft covering the opening of the large perineal sac and anus.

Female

Sows have a ‘Y’-shaped perineum. The urethral orifice lies cranially in between the branches of the Y. The vulva lies at

Figure 9.1 • Guinea pig (*Cavia porcellus*).

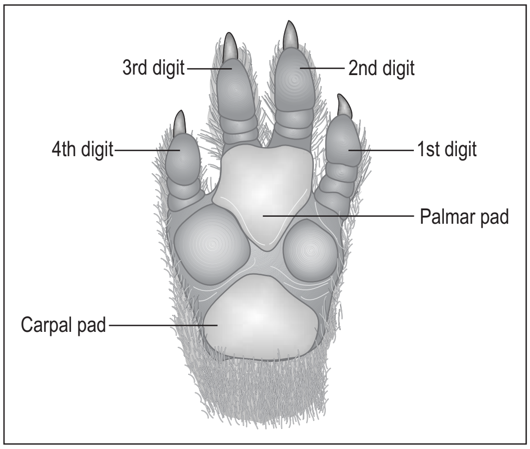


Figure 9.2 • Palmar surface of right forefoot of the guinea pig.

the intersection of the branches and has a 'U'-shaped orifice. It is covered by a vaginal membrane during anestrus and is bordered laterally by labia. Behind this is the perineal sac, which contains two perineal glands and which is often filled with hair, debris, and oily secretions. The anus is located at the base of the Y. Figure 9.4 shows the male and female genitalia.

SKELETAL SYSTEM

Skull

Guinea pigs have large tympanic bullae and prominent zygomatic arches (Fig. 9.7). The mandible, which is the largest bone in the skull, is united rostrally at the mandibular symphysis. It is roughened laterally for the insertion of the masseter muscle.

Axial skeleton

There are 7 cervical, 13–14 thoracic, 6 lumbar, 3–4 sacral and 4–7 caudal vertebrae. There are 13–14 pairs of ribs, with the last 2 being cartilaginous. The first six pairs articulate with the sternum, ribs 10–13/14 being floating ribs (Breazile & Brown 1976; Cooper & Schiller 1975b)(Figs. 9.5 and 9.6).

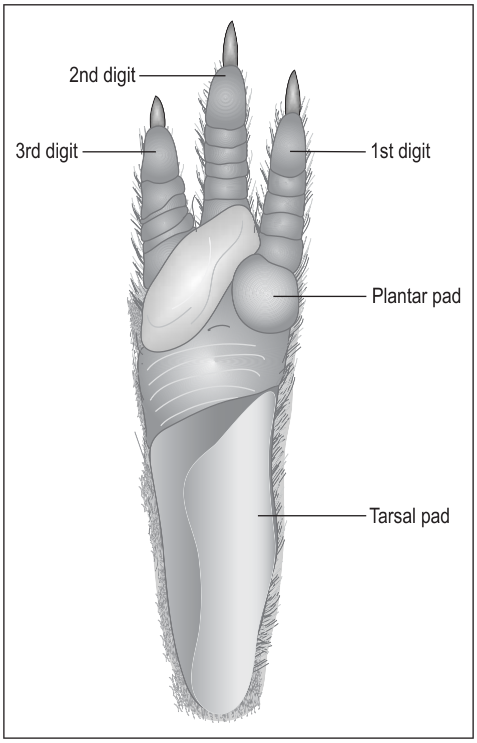


Figure 9.3 • Plantar surface of right hind foot of guinea pig.

Appendicular skeleton

The guinea pig has two tiny clavicles at the base of the neck and the acromion process of the scapula has an 'L'-shaped hamate process. The bones of the forelimb are the humerus, radius and ulna, nine carpal bones, four metacarpal bones, and four digits.

The os coxa results from the fusion of four bones shortly after birth: the ilium, ischium, pubis, and acetabular bone. Each bone contributes to the formation of the acetabulum. There are sexual variations in the pubic symphysis. Immature males and females have a fibrocartilage articulation which becomes ossified over 1 year of age. In primiparous female guinea pigs the pubic symphysis remains cartilaginous so that it can dilate to allow the relatively large fetus to pass through. These pubic bones separate 2 weeks before parturition to allow the passage of the large fetus. Palpation of this can be a useful guideline for estimating time of parturition (Breazile & Brown 1976; Cooper & Schiller 1975b).

The hindlimb is composed of femur, tibia, fibula, eight tarsal bones, three metatarsals, and three digits that each have three phalanges. The patella is large. The thin fibula articulates proximally with the lateral condyle of the tibia and distally with the calcaneus.

Os penis

This is a small, thin rodlike bone that lies within the glans of the penis (Cooper & Schiller 1975b).

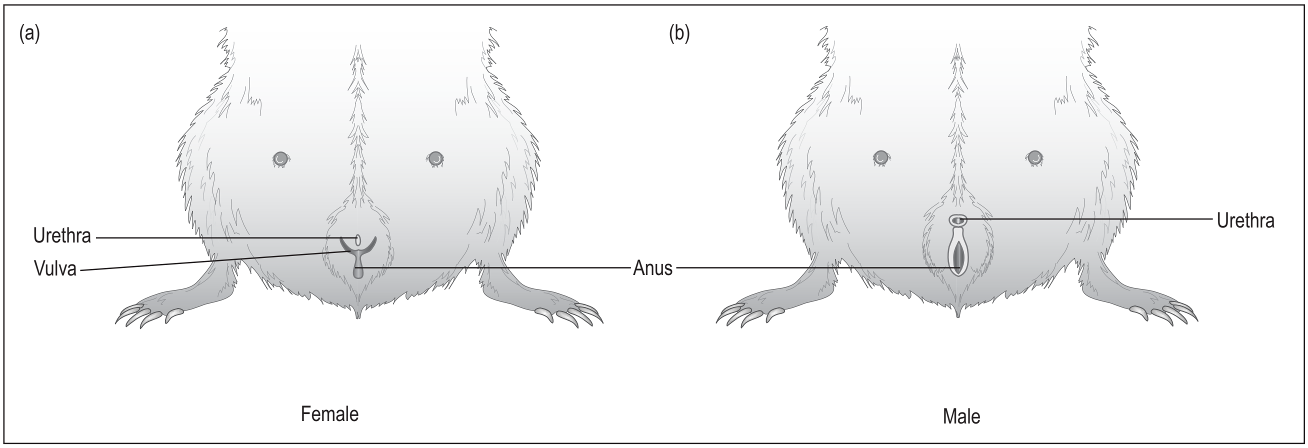

(a)
(b)
Urethra
Vulva
Anus
Urethra
Female
Male

Figure 9.4 • External genitalia.
a) Female – There is a 'Y'-shape with the vulva at the intersection of the branches and the anus distal to this. The urethral orifice lies between the branches of the Y.
b) Male – The cranial orifice is the penile urethra, covered by preputial folds. Caudally is a longitudinal cleft covering the opening of the large perineal sac and anus.

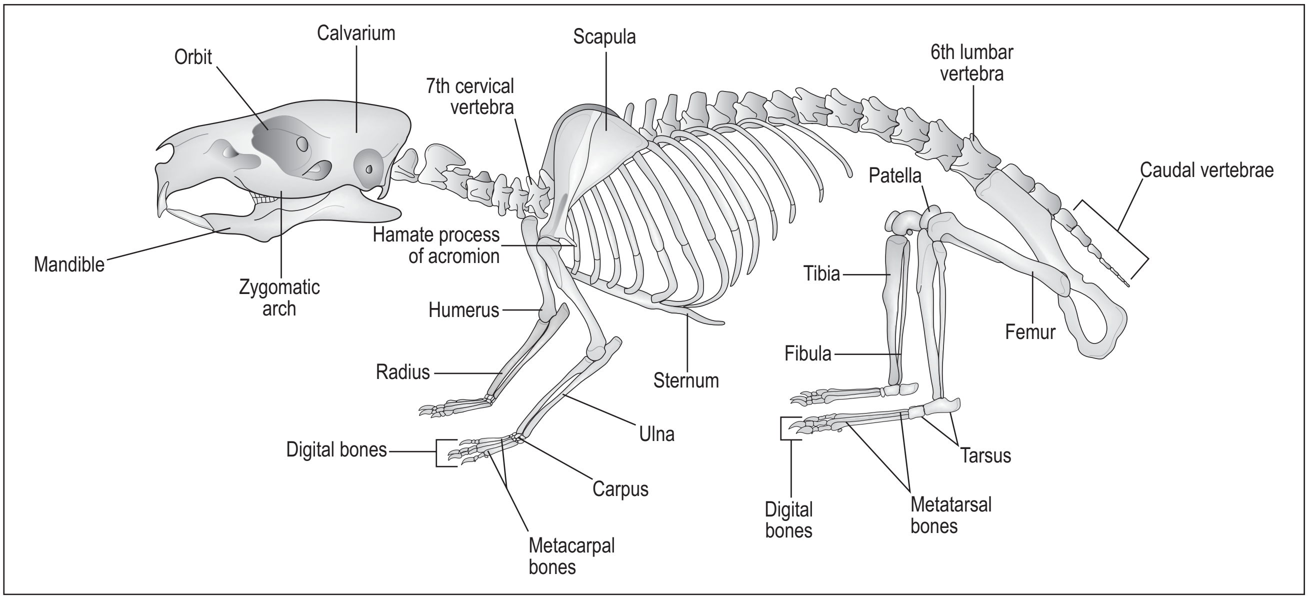

Orbit
Calvarium
Scapula
7th cervical vertebra
6th lumbar vertebra
Patella
Caudal vertebrae
Mandible
Zygomatic arch
Hamate process of acromion
Humerus
Radius
Digital bones
Metacarpal bones
Carpus
Ulna
Sternum
Tibia
Fibula
Femur
Digital bones
Metatarsal bones
Tarsus

Figure 9.5 • Skeleton of guinea pig (*Cavia porcellus*) with major bones labeled. From Popesko, P., Rajtova, V., & Horak, J. (1990) A colour atlas of anatomy of small laboratory animals. Vol. 1. Aylesbury, UK: Wolfe with permission.

CARDIOVASCULAR SYSTEM

The heart occupies a relatively large space in the thoracic cavity. It lies in the midline at the level of 2nd–4th intercostal space. The pericardium has two layers: an outer fibrous layer and a thinner serous layer.

Venepuncture

The blood volume of a guinea pig is 70–75 ml/kg of blood. The lateral saphenous and cephalic veins are most accessible but are small. The jugular vein, which lies in the superficial fascia of the ventral neck, can be used for larger blood samples. Compared to the rabbit, rat, and hamster the guinea pig has a longer prothrombin time, so blood clotting on sampling is less of a problem (Sisk 1976).

Unique blood cell features

Lymphocytes

The lymphocyte, which is the predominant peripheral blood cell, is resistant to steroids, as it is in the ferret, man, and monkey. This means that in contrast to the hamster, rabbit, and rat, treatment with steroids does not cause marked

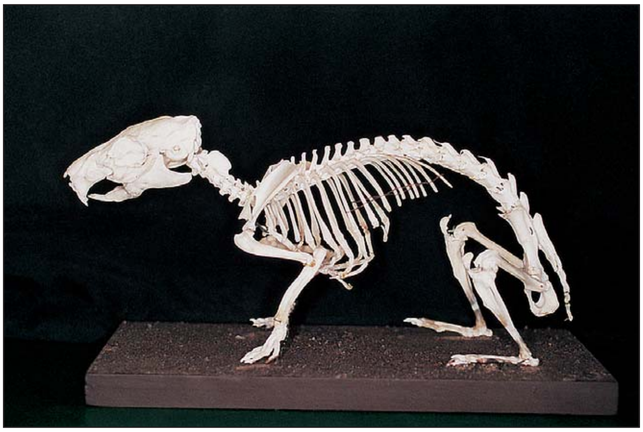


Figure 9.6 • Skeleton of guinea pig (*Cavia porcellus*).

changes in thymic physiology or peripheral lymphocyte counts (Sisk 1976).

Kurloff cell

This is a unique leukocyte of guinea pigs produced by the thymus under estrogen stimulation. It resembles a lymphocyte but contains oval or round inclusions called Kurloff bodies. These cells are rare in young animals, low in males and related to the estrous cycle in females. They are highest in the female during pregnancy and may play a role in the maternal–fetal barrier. They are also found in high number in the trophoblast region of the placenta (Percy & Barthold 2001; Sisk 1976).

Kurloff cells also appear to have cytotoxic effect on leukemic cells and may explain why spontaneous tumors are not common in guinea pigs (Percy & Barthold 2001).

RESPIRATORY SYSTEM

The caudodorsal part of the nasal cavity is lined by sensitive olfactory epithelium and this gives the guinea pig a keen sense of smell. The larynx is typical of all mammals in that it has five cartilages but there is no laryngeal ventricle. In spite of their wide vocal variety, guinea pigs have small and poorly developed vocal cords (Breazile & Brown 1976).

The caudal tongue is continuous with the soft palate, except for the *palatal ostium* (previously called the interpharyngeal ostium) in the middle (Fig. 9.8). This aperture forms the only connection between the oropharynx and the pharynx. The folds of soft palate around this hole are called the *velopharyngeal recess* (Timm et al. 1987).

CLINICAL NOTE

Although it is possible to perform endotracheal intubation in the guinea pig, take care to access the palatal ostium lying centrally; a lateral slip could cause damage to the vascular velopharyngeal folds.

The heart occupies a disproportionately large part of the thorax and leaves only a narrow space for the lungs on each side. The right lung has four lobes (cranial, middle, accessory, and caudal) that are separated by a deep fissure. The left lung has three lobes: cranial, middle, and caudal (Breazile & Brown 1976).

IMMUNE SYSTEM

Lymph nodes

The lymph nodes are oval (or bean shaped) red-brown nodules located within the lymphatic vessels. They are covered by a smooth transparent capsule, and blood vessels, nerves and lymphatic vessels enter at a tiny depression called the *hilus*.

The mandibular lymph nodes consist of 2–4 nodes lying along the ventral border of the mandible. The cervical lymph nodes are around 5–8 mm diameter and located in adipose tissue cranial to the scapula. The deep nodes lie adjacent to the trachea between the internal and external jugular veins. In young animals it is covered by the thymus.

CLINICAL NOTE

Harsh abrasive foods can pierce the oral mucosa and enable *Streptococcus zooepidemicus*, a normal oral pathogen, to access the cervical lymph nodes and cause abscessation. Guinea pigs present with pus-filled ventral cervical lymph nodes which need lancing or, in severe cases, surgical removal (Huerkamp et al. 1996).

Thymus

The cervical thymus is so readily accessible that the guinea pig has been used extensively for immunology research. In immature animals it is located in the cranial mediastinum and subcutaneously in the neck where it surrounds the trachea ventrally and laterally. It is composed of two yellow-brown, oval lobes extending from the angle of the mandible to approximately half way to the thoracic inlet. In the adult it becomes mainly replaced by fat (Breazile & Brown 1976; Harkness & Wagner 1995).

Spleen

The spleen is relatively large compared to that found in most rodents and rabbits. It lies on the left side, lateral to the greater curvature of the stomach and attached by the gastrosplenic ligament (Breazile & Brown 1976).

DIGESTIVE SYSTEM

Feeding behavior

Guinea pigs are crepuscular and thus feed at dawn and dusk. They are strict herbivores with molar teeth suited for grinding vegetative matter and, like rabbits, exhibit cecotrophy. They are also fastidious eaters that learn early in life what to eat.

Guinea pigs grab stalks by the base and tear them off by a backward and upward thrust of the head. In the wild much of the guinea pig's water requirements would come through its greens, but in captivity water must be supplied.

CLINICAL NOTE

When supplied with a water bottle guinea pigs do not lick the drops but put their whole mouths around the nozzle, creating a slurry which can easily block it. This can lead to rapid dehydration in guinea pigs fed solely on dry food diets.

Digestive physiology

The normal gastric emptying time is 2 hours and total gastrointestinal transit time averages 20 hours (range 8–30 hours). If cecotrophy is accounted for then total transit time is 66 hours. Cecotrophy is performed 150–200 times daily and is essential for fiber and protein digestion (Ebino 1993). Young guinea pigs initially populate their gut by eating the sow's droppings. The gut flora is mainly gram-positive bacteria and anaerobic lactobacillus, but coliforms, yeasts, and clostridia are also present in small numbers (Cheeke 1987; Harkness & Wagner 1995; Huerkamp et al. 1996).

Guinea pigs digest fiber more efficiently than rabbits (Cheeke 1987). Unlike in rabbit and rats, satiety in guinea pigs is governed by the distension of the gastrointestinal tract as appetite does not increase with added cellulose to the diet (Cheeke 1987; Harkness 1990; Harkness & Wagner 1995). A crude protein level of 18–20% is needed for growth and lactation, and a minimal crude fiber level is 10% (Huerkamp et al. 1996).

Vitamin C

Guinea pigs lack the enzyme L-gulonolactone oxidase, which synthesizes ascorbic acid from glucose. Ascorbic acid is necessary for the production of hydroxylysine and hydroxyproline, both essential for collagen synthesis in connective tissues. Abnormal collagen results in leaking blood vessels and hemorrhage in the joints, gums, and intestines. Collagen also anchors the teeth in the sockets so hypovitaminosis C can lead to dental problems (Cheeke 1987; Huerkamp et al. 1996; Navia & Hunt 1976).

Adult non-breeding guinea pigs need 5 mg/kg of vitamin C daily in their diet (Harkness & Wagner 1995). Young growing animals have the highest demand for vitamin C; scurvy can develop within 2 weeks on a deficient diet.

Metastatic mineralization

The guinea pig lays down soft tissue calcification with relative ease. Why this occurs is unclear but it may be related to dehydration and mineral imbalances. Lesions can be seen in animals over 1 year of age (Huerkamp et al. 1996).

CLINICAL NOTE

When supplementing guinea pigs with vitamin C it is important to avoid any human multivitamin products as these can be too high in Vitamin D and lead to metastatic calcification (Huerkamp et al. 1996).

Dentition

There are 20 teeth and the dental formula is 1/1, 0/0, 1/1, 3/3. All teeth are rootless (aradicular) and constantly growing (Vaughan 1986). As a consequence of this malocclusion can occur in both molars and incisor teeth. The chisel-shaped incisors are white. The maxillary cheek teeth are angled laterally, the lower teeth are arched medially toward the tongue (Breazile & Brown 1976; Cooper & Schiller 1975b).

CLINICAL NOTE

In guinea pigs with molar malocclusion the maxillary cheek teeth overgrow laterally into the buccal mucosa while the mandibular cheek teeth arch medially, causing tongue entrapment and subsequent anorexia.

Oral cavity

The oral cavity is small and there is a large elongated tongue. The upper and lower cheek folds can fold inwards during gnawing, dividing the mouth into two regions. Caudally the mouth communicates with the pharynx and is lubricated by salivary glands.

The tongue is large and elongated and covers most of the floor of the mouth and oropharynx. It is bounded laterally by the mandible. The rostral two thirds lie free and caudally it is raised into a mound where there are extensive papillae (Cooper & Schiller 1975c). The muscles of mastication are well developed, reflecting the gnawing and grinding behavior of this species (Breazile & Brown 1976).

Salivary glands

There are five pairs of salivary glands: parotid, mandibular, zygomatic, major and minor sublingual. The ducts enter the oral cavity near the molar teeth. The two mandibular glands

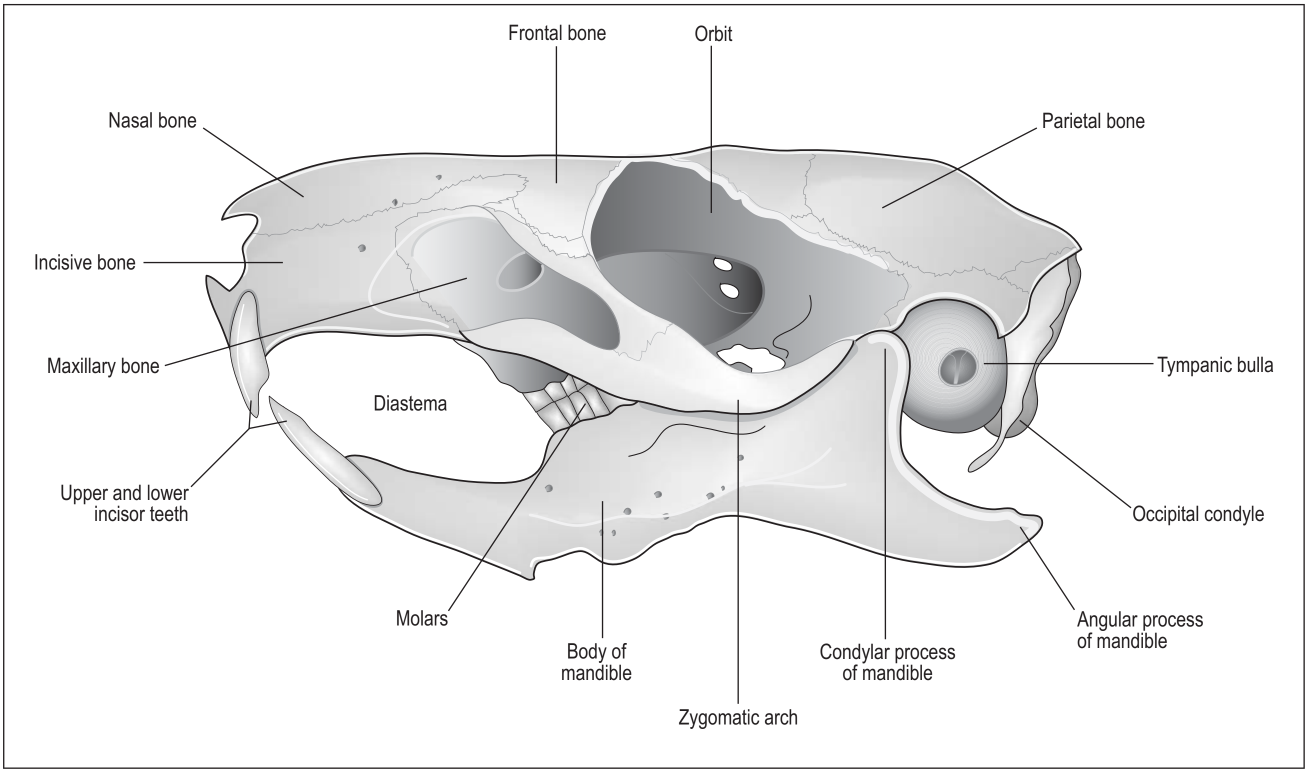

Frontal bone
Orbit
Nasal bone
Parietal bone
Incisive bone
Maxillary bone
Diastema
Tympanic bulla
Upper and lower incisor teeth
Occipital condyle
Molars
Body of mandible
Condylar process of mandible
Angular process of mandible
Zygomatic arch

Figure 9.7 • Lateral view of guinea pig skull. From Popesko, P., Rajtova, V., & Horak, J. (1990) A colour atlas of anatomy of small laboratory animals. Vol. 1. Aylesbury, UK: Wolfe with permission.

come in contact with each other in the ventral midline (Breazile & Brown 1976; Timm et al. 1987).

Pharynx

The nasopharynx and oropharynx are separated by the soft palate, which communicates with the oral cavity via the palatal ostium (see Respiratory system) (Timm et al. 1987). Guinea pigs do not have tonsils but have lymphoid nodules in folds in the wall of the pharynx.

Esophagus

This runs dorsal to the trachea in the midline and lies to the left as it enters the thoracic inlet. It is lined by stratified squamous epithelium, proximally by striated muscle, and distally by smooth muscle. It enters the cardiac portion of the stomach at an oblique angle near the lesser curvature.

Stomach

Guinea pigs are mongastric but, unlike the rat and hamster, their stomach is completely glandular. The stomach lies in the left cranial portion of the abdomen. The lesser curvature of the stomach is very small and the angle formed by it and the esophagus is called the angular notch. The greater and lesser omentum extend from the stomach, as in other species (Cooper & Schiller 1975c).

Intestines

The small intestine occupies the right side of the abdomen and measures about 125 cm in length. There is little to distinguish the different parts of the intestine. Lymphoid nodules (Peyer patches) are found in the lamina propria. The large intestine begins at the ileocecal valve and terminates at the anus (Breazile & Brown 1976; Cooper & Schiller 1975c).

Cecum

The cecum is a large, thin-walled, green-brown sac filling most of the left ventral abdominal cavity (Fig. 9.9). This is the largest dilation of the alimentary canal, being 15–20 cm long and containing 65% of the gastrointestinal contents. Externally, three white muscular longitudinal bands are visible: the dorsal, ventral and medial teniae coli. These being shorter than the cecum create saccular outpouchings called haustra (Cooper & Schiller 1975c).

Colon

The colon is dark green and 70 cm long. Although it has an ascending, transverse, and descending portion named accord-

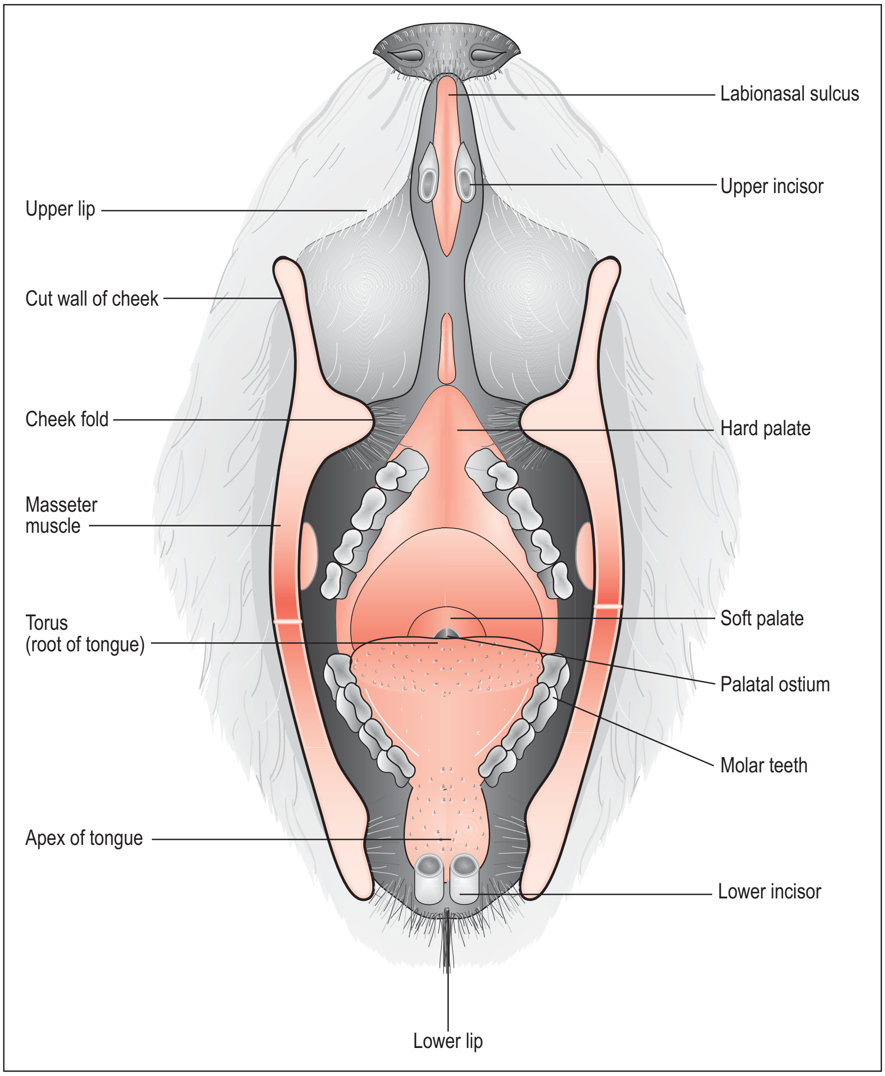


Figure 9.8 • Open mouthed view of guinea pig showing molar teeth and palatal ostium. From Popesko, P., Rajtova, V., & Horak, J. (1990) A colour atlas of anatomy of small laboratory animals. Vol. 1. Aylesbury, UK: Wolfe with permission.

ing to location in the abdominal cavity, it is functionally divided into the proximal (20 cm) and distal colon (50 cm).

The proximal colon plays a role in separating digesta into fecal pellets and cecotrophs. Although there are no haustra outpouchings as in the rabbit, the mesenteric side of the colonic mucosa folds to form a longitudinal furrow. This furrow aids in separating the high protein digesta from the poor quality protein destined to become fecal pellets. In the proximal colon this furrow becomes very deep and is lined by mucous cells which trap bacteria and high protein particles. These are then transported by antiperistalsis back to the cecum for further fermentation (Cheeke 1987; Holtenius & Bjornhag 1985).

Liver

The liver is the largest gland, is red-brown in color, and smooth. There are six lobes: right, medial, left lateral, left medial, caudate, and quadrate. The gall bladder is well developed and lies medially in the quadrate lobe (Breazile & Brown 1976; Cooper & Schiller 1975c).

Pancreas

This is triangular, pink-red and has three lobes. It lies in contact with the descending duodenum.

URINARY SYSTEM

The kidneys lie retroperitoneally on either side of the midline and are often surrounded by dense adipose tissue on the caudal and medial borders. In the female the broad ligament, which also contains abundant fat, is attached to the ventral aspect of the kidney. The left kidney is more caudal than the right. The renal pelvis is large and there is a single longitudinal papilla (Breazile & Brown 1976; Cooper & Schiller 1975d).

The urinary bladder is large, saclike and triangular in shape (Cooper & Schiller 1975d). The alkaline urine is thick

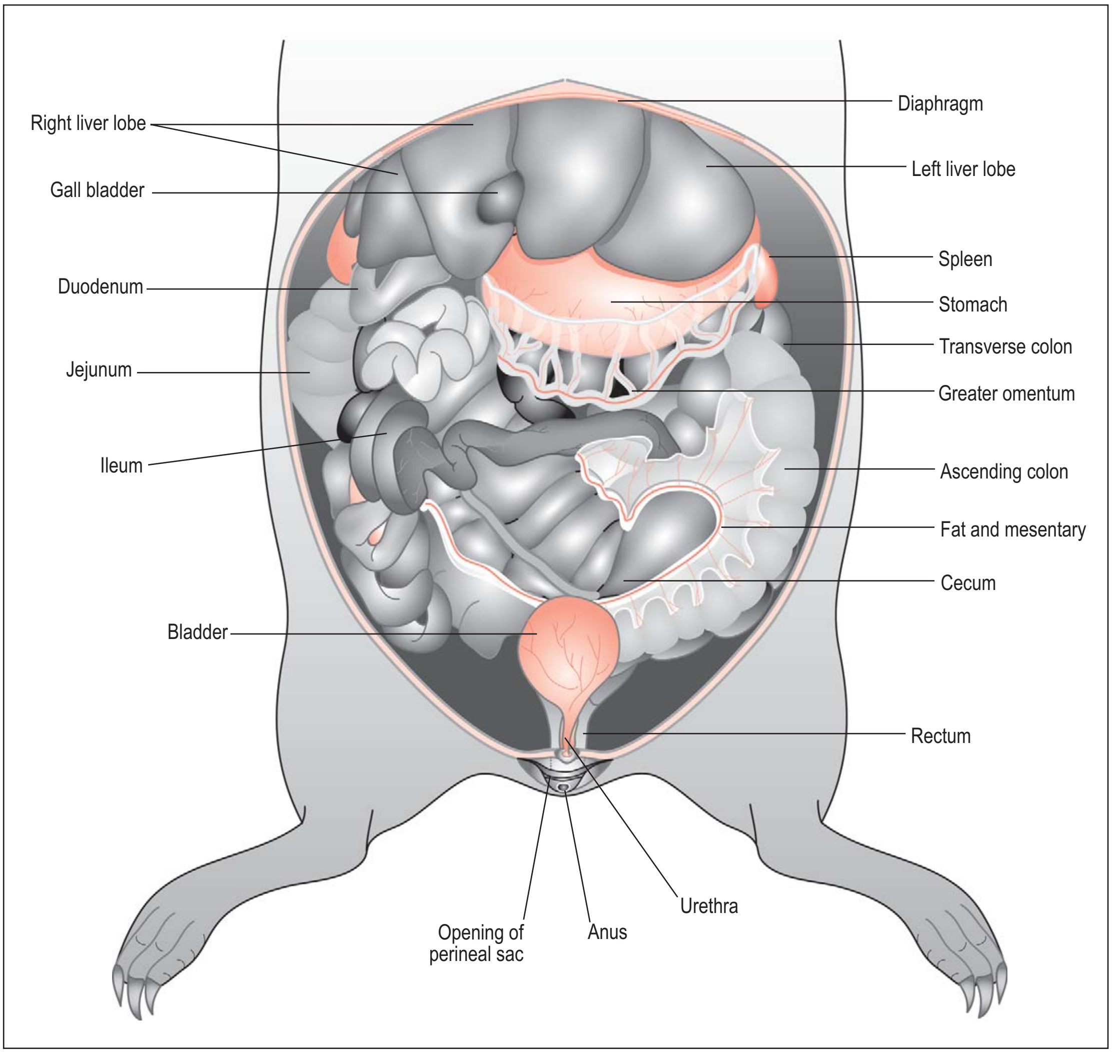

Right liver lobe
Gall bladder
Duodenum
Jejunum
Ileum
Bladder
Diaphragm
Left liver lobe
Spleen
Stomach
Transverse colon
Greater omentum
Ascending colon
Fat and mesentary
Cecum
Rectum
Urethra
Anus
Opening of perineal sac

Figure 9.9 • Ventral view of abdominal viscera of guinea pig.

and cloudy white, containing calcium carbonate and ammonium phosphate crystals. In the female the external urethra is separate from the vagina.

REPRODUCTIVE SYSTEM

Male

The male genital organs consist of the testes, accessory sexual glands, and the perineal and caudal glands. The perineal sac glands are present in both sexes but are more extensive in the male. They lie on either side of the anus and contain extensive caseous secretions, hair and skin debris (Cooper & Schiller 1975a).

The inguinal ring is permanently open. The scrotum contains the testes, epididymis, and caudal spermatic cord. The epididymis lies along the dorsolateral margin and has large fat bodies associated with its head and tail. The distal extremity of the penis contains an os penis that has two horny prongs of equal length lying in a pouch just caudoventral to the urethral opening. During erection this pouch is everted to project the two prongs. Androgen levels decrease rapidly following castration although sexual mounting behavior can last some weeks (Breazile & Brown 1976; Cooper & Schiller 1975d).

Accessory glands

These consist of the prostate gland, coagulating gland, seminal vesicles, and bulbourethral glands (Fig. 9.10). The paired seminal vesicles are large, yellow-white vermiform sacs lying in the caudal peritoneal cavity, dorsal to the bladder, and extending 10 cm cranially into the abdomen. As they are large and filled with semi-solid seminal secretions they could be confused with the female uterus. The coagulating and prostate glands lie close to the base of the vesicles. The bulbourethral glands are oval, paired glands which lie close to the urethra at the ischial arch (Cooper & Schiller 1975d).

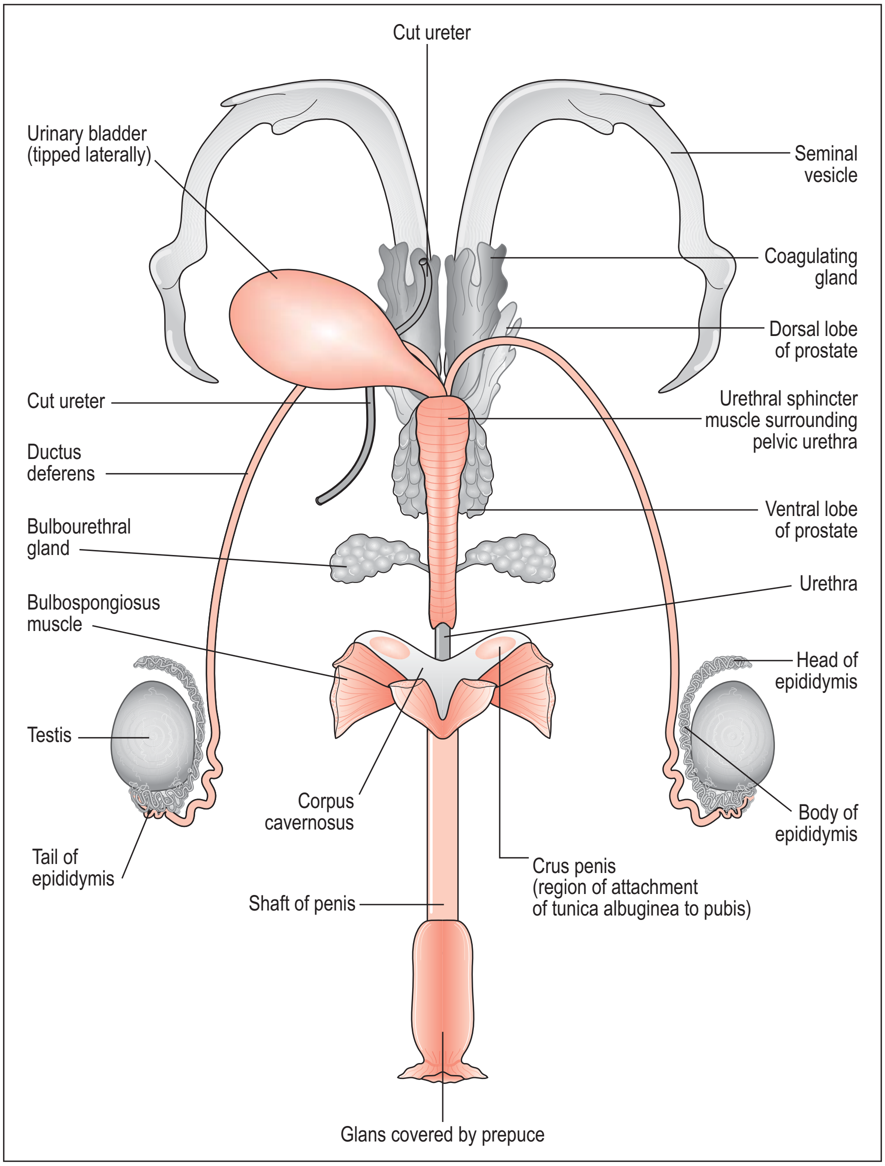

Cut ureter
Urinary bladder (tipped laterally)
Seminal vesicle
Coagulating gland
Dorsal lobe of prostate
Cut ureter
Urethral sphincter muscle surrounding pelvic urethra
Ductus deferens
Ventral lobe of prostate
Bulbourethral gland
Urethra
Bulbospongiosus muscle
Head of epididymis
Testis
Body of epididymis
Corpus cavernosus
Tail of epididymis
Crus penis (region of attachment of tunica albuginea to pubis)
Shaft of penis
Glans covered by prepuce

Figure 9.10 • Ventral view of the male genital tract showing large seminal vesicles.

CLINICAL NOTE

Because the male urethra transports copious seminal fluid as well as urine, aged male guinea pigs can develop cystitis and even obstructions due to occlusion of the penile urethra with coagulated seminal secretions or calculi.

Female

The ovaries are located caudolateral to the kidneys and are supported by a short mesovarium. The oviduct lies in close contact within the ovarian bursa. There is a pink bicornate uterus, a short uterine body, and a single cervix opening into the vagina (Cooper & Schiller 1975d) (Fig. 9.11). The broad ligament (mesovarium, mesosalpinx, and mesometrium) contains a lot of fat, which makes identification of the ovarian pedicle difficult during ovariohysterectomy.

Like in most mammals, an anastomosis between the ovarian artery (a branch of the aorta) and the uterine artery (a branch of the internal iliac) occurs in the uterine mesentery. The uterine artery provides the main blood supply to the ovary (Del Campo & Ginther 1972; Harkness & Wagner 1995).

A unique feature of caviomorphs is the presence of a vaginal membrane. This is a thin, translucent epithelial membrane that seals the vaginal orifice except during copulation and parturition. It closes shortly after estrus or, if copulation has taken place, after expulsion of the vaginal plug (Breazile & Brown 1976; Cooper & Schiller 1975d).

Estrus

Guinea pigs are polyestrous, with an estrous cycle of 15–17 days (Harkness & Wagner 1995; Nowak 1999). Estrus

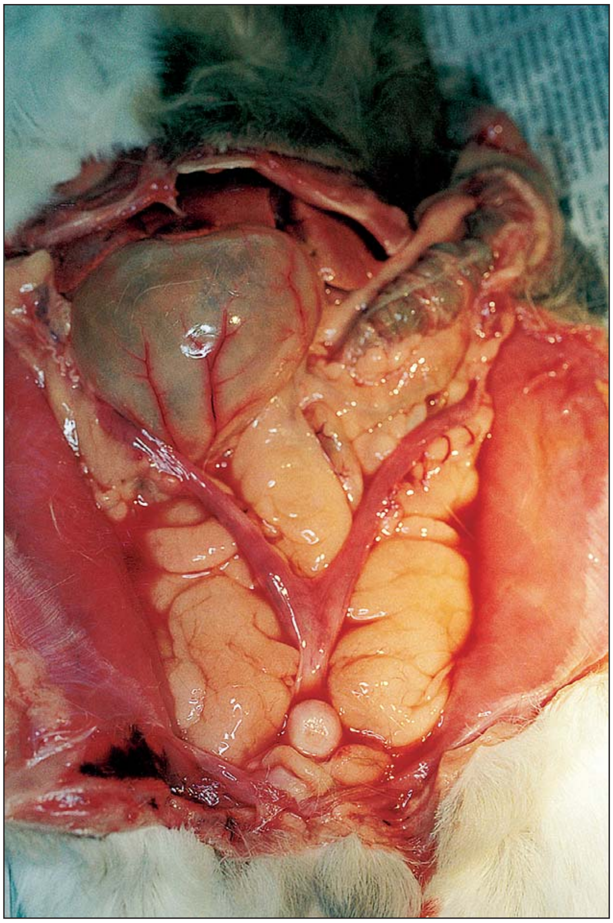


Figure 9.11 • Bicornate uterus of 2-year-old guinea pig sow.

lasts from 6–11 hours during which time the female shows lordosis, elevation of the rump, and dilation of the vulva. The vaginal membrane opens for about 2 days during this time and closes after ovulation. A thick mucus discharge can be seen. Ovulation is spontaneous and usually occurs about 10 hours into the cycle. A fertile post partum estrus lasts from 2–10 hours after parturition.

Mammary glands

There is a single pair of inguinal mammary glands. These are divided into fine lobules, which open via a number of small ducts into one large duct to the exterior. There are two teats. In pigmented animals these glands are usually dark and hairless. The left and right mammary glands do not have a common blood supply, making mammectomy easier. Although the male has two teats the mammary glands are rudimentary (Breazile & Brown 1976; Cooper & Schiller 1975d).

Sexual maturity

Puberty occurs at 2 months in the female and 3 months in the male, although males will show mounting behavior from the age of only 1 month. Females have, however, become pregnant at as early as 4–5 weeks (Nowak 1999).

CLINICAL NOTE

Cystic ovaries are common and have been identified on post mortem in 76% of female guinea pigs from 2–5 years of age (Figs. 9.12 and 9.13). They develop spontaneously and can range in size from 0.5–7.0 cm. Both ovaries are usually affected and may be single or multiloculate, and filled with clear fluid. The most effective treatment is ovariohysterectomy, preceded if necessary by percutaneous ovarian drainage.

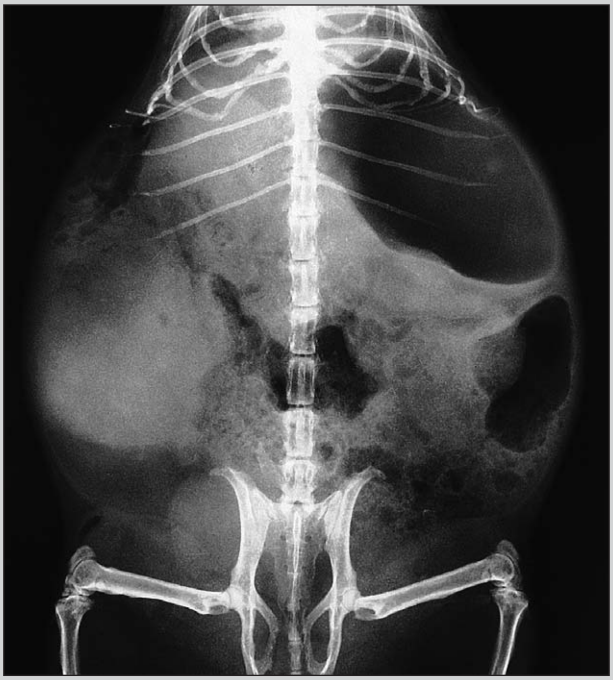


Figure 9.12 • Ventrodorsal radiograph of guinea pig with abdominal distension. Cystic ovaries were diagnosed on ultrasound. Note non-fusion of pubic symphysis.

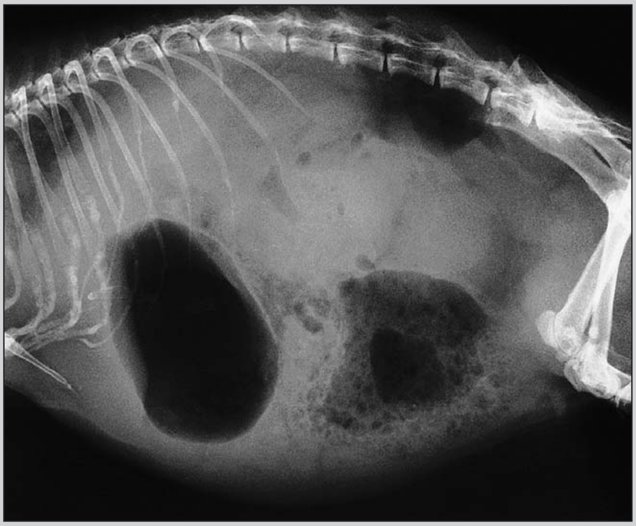


Figure 9.13 • Lateral radiograph of the guinea pig in Fig. 9.12.

Copulatory plugs

These are formed from secretions of the male seminal vesicles and sloughed vaginal epithelium. They help to prevent sperm leakage after copulation and prevent fertilization of the female by subsequent males. This plug will usually fall out of the vagina and can be found as a waxy mass on the floor a few hours post mating.

Gestation

Gestation is 59–72 days and is shorter in primiparous sows and small litters. Implantation occurs on day 6–7. The placenta is hemochorial, meaning that, as in humans, rabbits, and hamsters, the trophoblast is in contact with maternal blood supply. It is also thought that Kurloff cells may play a role in protection of fetal cells (see Cardiovascular system). The placenta secretes progesterone on day 15 and fetuses can be palpated as early as this. Guinea pigs receive all maternal antibodies from the placenta and not from colostrum (Sisk 1976).

In the latter half of the pregnancy the cartilage joining the pubic symphysis begins to dilate under the effects of the hormone relaxin. Two days before parturition the gap widens to 15 mm. By the time of parturition, the cartilage is gone and the pubis widens to about 25 mm (over 50 times its normal width) (Harkness & Wagner 1995; Sisk 1976).

Parturition and lactation

Birth weights vary from 45–115 g and are inversely related to litter size. The placenta is eaten by the dam and other guinea pigs. The young are weaned at a body weight of 180 g, or at 21 days of age. Milk production peaks 5–8 days post partum and ceases between days 18 and 23. Guinea pig milk consists of 4% fat, 8% protein, and 3% lactose (Harkness & Wagner 1995; Sisk 1976).

CLINICAL NOTE

Sows which are bred after 7–10 months of age do not get the same widening of the pubic bones so dystocia commonly results (Huerkamp et al. 1996).

ENDOCRINE SYSTEM

The adrenal glands are associated with the craniomedial surface of each kidney and are particularly large. Each gland is roughly triangular, bilobed, and yellow-brown in color.

SENSES

Hearing

The cartilage ear canal is long and tortuous, making it difficult to visualize the tympanic membrane. The large tympanic bulla which contains the middle and inner ear gives the guinea pig excellent hearing (Harkness & Wagner 1995).

Sight

The eyes are located in the shallow, bony orbits and lie laterally in the mid portion of the skull. They have a combined visual field of 340 degrees. The eye is embedded in fat and glandular tissue. The upper and lower eyelids protect the eye and blinking is only occasional. Unlike the rabbit, there are lacrimal puncta at both the upper and lower eyelids. The nictitating membrane is rudimentary and is just a small pigmented fold.

Orbital contents

The globe is embedded in fat and actually makes up less than half the orbit; the rest is occupied by the extraocular muscles, the lacrimal glands, zygomatic salivary gland, blood vessels, and nerves (Cooper & Schiller 1975e).

The lacrimal gland lies at the caudoventral aspect of the orbit. It drains via two canaliculi into the lacrimal sac at the rostral orbit margin. The nasolacrimal duct is quite wide but narrows near the nasal vestibule where it terminates. A richly venous ophthalmic plexus, made up of branches of the maxillary and ophthalmic veins, surrounds the eyeball (Cooper & Schiller 1975e).

Olfaction

Olfactory cells in the nose connect with the olfactory nerve and penetrate the cribriform plate of the ethmoid bone to pass dorsally into the olfactory bulbs of the brain.

INTEGUMENT

Guinea pigs are born fully haired. The hair consists of large, coarse guard hairs with a fine undercoat. A prominent hairless area, measuring about 2.5 to 4 cm in diameter lies just caudal to the pinna on both sides. This area lacks sebaceous and sweat glands and is more darkly pigmented than the remaining skin. It is larger in albino guinea pigs.

Coat color

Guinea pigs can be one uniform color or mixed. The original natural color, *agouti*, is a combination of black and brown on each hair, but many colors are now possible. Albinos have red eyes with pink ears and feet. Himalayans have albino features at birth but develop dark points at the nose, ears, and feet. Brindle guinea pigs have a mixture of brown and black hairs.

Coat variety

The Self variety has smooth, short hairs lying in parallel segments. The Abyssinian has short hairs arranged in whorls that make its coat look uneven. When the periphery of these whorls meet in the midline it gives a crested or mohican appearance. Hair length for the Self and Abyssinian is around 35 mm but the Peruvian can grow hair as long as 200 mm, and the latter are mainly used as show animals (Cooper & Schiller 1975a).

Vibrissae

These are long hairs used as tactile organs and there are seven groups divided according to their location. The buccal vibrissae lie in six parallel rows above the upper lip and are directed backwards from the muzzle. Two mental vibrissae lie on the chin while two nasal ones are located dorsolaterally on each side of the nose. Four supraorbital ones lie just rostral and dorsal to each upper eyelid and three infraorbital ones lie inferior and rostral to each lower eyelid (Cooper & Schiller 1975a).

Sebaceous glands

These are numerous along the dorsum and around the anus. The perineal glands are used for scent marking and contain a lot of sebaceous material. There are no anal glands. The caudal sebaceous gland sited at the coccyx lies 1 cm dorsal to the anus and is seen as an oval region that secretes pheromones and which becomes matted with sticky hair in adult males (Breazile & Brown 1976).

KEY POINTS

- Incisors and molars are open rooted, hence dental disease is common.
- Vitamin C is essential and scurvy can develop within 4 days of decreased intake.
- Males have a prominent caudal sebaceous gland and very large seminal vesicles.
- Females have a bicornate uterus, vaginal membrane, and separate urethral and vaginal orifices.
- The left and right mammary glands have separate blood supplies.
- The pubic symphysis dilates for parturition. Females should be bred before 7–10 months to prevent fusion and subsequent dystocia.

REFERENCES

Breazile, J. E., & Brown, E. M. (1976) Anatomy. In J. E. Wagner & P. J. Manning (eds.), *The biology of the guinea pig*. New York: Academic Press. pp. 53–62.

Cheeke, P. R. (1987) Nutrition of guinea pigs. In T. J. Cunha (ed.), *Rabbit feeding and nutrition*. Orlando, Fla.: Academic Press. pp. 344–353.

Cooper, G., & Schiller, A. L. (1975a) *Anatomy of the guinea pig*. Cambridge, Mass.: Harvard University Press. External Anatomy; pp. 3–17.

Cooper, G., & Schiller, A. L. (1975b) *Anatomy of the guinea pig*. Cambridge, Mass.: Harvard University Press. The skeletal system; pp. 17–71.

Cooper, G., & Schiller, A. L. (1975c) *Anatomy of the guinea pig*. Cambridge, Mass.: Harvard University Press. The digestive system; pp. 303–324.

Cooper, G., & Schiller, A. L. (1975d) *Anatomy of the guinea pig*. Cambridge, Mass.: Harvard University Press. The urogenital system; pp. 325–357.

Cooper, G., & Schiller, A. L. (1975e) *Anatomy of the guinea pig*. Cambridge, Mass.: Harvard University Press. The eye and orbital contents; pp. 369–389.

Del Campo, C. H., & Ginther, O. J. (1972) Vascular anatomy of the uterus and ovaries and the unilateral luteolytic effect of the uterus: Guinea pigs, rats, hamsters and rabbits. *American Journal of Veterinary Research 33*, 2561–2578.

D'Erchia, A. M., Gissi, C., Pesole, G., et al (1996) The guinea pig is not a rodent. *Nature 381*, 597–599.

Ebino, K. Y. (1993) Studies on coprophagy in experimental animals. *Experimental Animals 42*, 1–9.

Harkness, J. E. (1990) *Rabbits and rodents laboratory animal science*. *University of Sydney Proceedings 142*. Nutrition of rabbits and rodents; pp. 99–111.

Harkness, J. E., & Wagner, J. E. (1995) *The biology and medicine of rabbits and rodents*, 4th edn. Baltimore: William & Wilkins. Biology and husbandry – the guinea pig; pp. 30–40.

Holtenius, K., & Bjornhag, G. (1985) The colonic separation mechanism in the guinea pig (*Cavia porcellus*) and the chinchilla (*Chinchilla laniger*). *Comparative Biochemistry and Physiology 82A*(3), 537–542.

Huerkamp, M. J., Murray, K. A., & Orosz, S. E. (1996) Guinea pigs. In K. Laber-Laird, M. M. Swindle & P. Flecknell (eds.), *Handbook of rodent and rabbit medicine*. Oxford: Pergamon. pp. 91–149.

Navia, J. N., & Hunt, C. E. (1976) Nutrition, nutritional diseases and nutrition research applications. In J. E. Wagner & P. J. Manning (eds.), *The biology of the guinea pig*. New York: Academic Press. pp. 235–267.

Nowak, R. M. (ed.) (1999) Cavies or guinea pigs. *Walker's Mammals of the World* , 6th edn. Vol. 11. Baltimore: John Hopkins University Press. pp. 1667–1669.

Percy, D. H., & Barthold, S. W. (2001) *Pathology of laboratory rodents and rabbits*, 2nd edn. Guinea pig; pp. 209–244.

Popesko, P., Rajtova, V., & Horak, J. (1990) *A colour atlas of anatomy of small laboratory animals*. Vol. 1. Aylesbury, UK: Wolfe. pp. 147–240.

Sisk, D. B. (1976) Physiology. In J. E .Wagner & P. J. Manning (eds.), *The biology of the guinea pig*. New York: Academic Press. pp. 63–92.

Timm, K. I., Jahn, S. E., & Sedgwick, C. J. (1987) The palatal ostium of the guinea pig. *Laboratory Animal Science 37*, 801–802.

Vaughan, T. A. (ed.) (1986) *Mammology*, 3rd edn. Philadelphia: Saunders College. Order Rodentia; pp. 244–277.

Wagner, J. E. (1976) Introduction and taxonomy. In J. E. Wagner & P. J. Manning (eds.), *The biology of the guinea pig*. New York: Academic Press. pp. 1–20.

Weir, B. J. (1974) Notes on the origin of the domestic guinea pig. *Symposia of the Zoological Society of London 34*, 437–446.

10

Rats

INTRODUCTION

The original habitat of the Norwegian or brown rat (*Rattus Norvegicus*) is Asia where they lived in burrows on the plains of north China and Mongolia. The black rat (*Rattus rattus*) comes from India and the Malaysian peninsula. In the Middle Ages the black rat spread to the rest of the world when trade routes opened from the East. The brown rat followed later, arriving in Europe in the early 18th century, and rat baiting became a popular sport. Following the routes of human migration it reached America by the end of the century (Harkness & Wagner 1995).

The brown rat became more successful due to its greater ability to withstand cold and live in close proximity to humans. Its omnivorous diet meant it could adapt to every environment from sewers to drains and buildings (Koolhaas 1999; Sharp & LaRegina 1998).

Rattus norvegicus was the first species to be domesticated purely for scientific purposes and is now the most widely studied experimental animal in biomedical research.

Longevity

The average life span of a rat is 2.5–3.5 years, with the females living longer, on average (Fallon 1996). Longevity can be increased by feeding a low fat and vegetable protein diet (Yu 1994).

THERMOREGULATION

Rats have few sweat glands and, being unable to pant, have poor heat tolerance. They do not increase their water intake at high ambient temperatures but instead try to cool down by increasing salivation and seeking shade (Bivin et al. 1979). Death occurs at temperatures over 37° C. The tail and ear are very important for heat dispersion, with blood vessels vasoconstricting and dilating according to ambient temperatures (Fallon 1996; Sharp & LaRegina 1998).

Adult brown rats have good tolerance to cold and can adapt extremely well to cold climates by laying down brown fat within 3 or 4 weeks. This can form extensive sheets of pink fatty tissue along the ventrolateral and dorsal aspects of the neck (Bivin et al. 1979; Greene 1962). Pups, however, have no intrinsic thermoregulatory mechanisms until the end of the first week of life and are kept warm by siblings and the mother (Fallon 1996; Koolhaas 1999).

CLINICAL NOTE

The vasodilation of the tail vessels can be used to advantage for venepuncture from the lateral tail vein. The rat should be kept at a warm ambient temperature and the tail immersed in warm water to dilate the blood vessels prior to sampling.

The preferred ambient temperature range for captive rats is 18–26° C and with a relative humidity of 40–70%. Unweaned rats that are less than 17 days old and kept at low humidity develop a condition called *ringtail*. This is where annular lesions on their tail causes the distal end to become necrotic and slough off.

Photoperiod

The rat is mainly nocturnal but will have cycles of activity by day as well as night. A photoperiod of 12 hours day, 12 hours night is recommended for captive rats (Baker 1979; Koolhaas 1999). Albino rats are light sensitive so bright lights should be avoided (Koolhaas 1999).

GENERAL EXTERNAL ANATOMY

The rat has a stocky body and a scaly tail that is about 85% of the body length (Fig. 10.1) (Bivin et al. 1979). The ears are small and covered with fine hairs. The male is larger than the female. The body weight of the male is 450 to 520 g and that of the female is 250 to 300 g.

Head

The upper lips are hairy and cover the incisors so that only the tips are visible. They are cleaved midline by a deep,

Figure 10.1 • The brown rat (*Rattus norvegicus*).

hairless philtrum. The nasal skin is also hairless and contains the slitlike nostrils, which can be closed under water. The space between the lips, cheeks, and teeth is called the *vestibule*.

Teeth

The incisors are used for fighting, holding food, excavating while burrowing, and gnawing. Iron pigments are responsible for the yellow-orange color of the incisors (Fallon 1996) (Fig. 10.2).

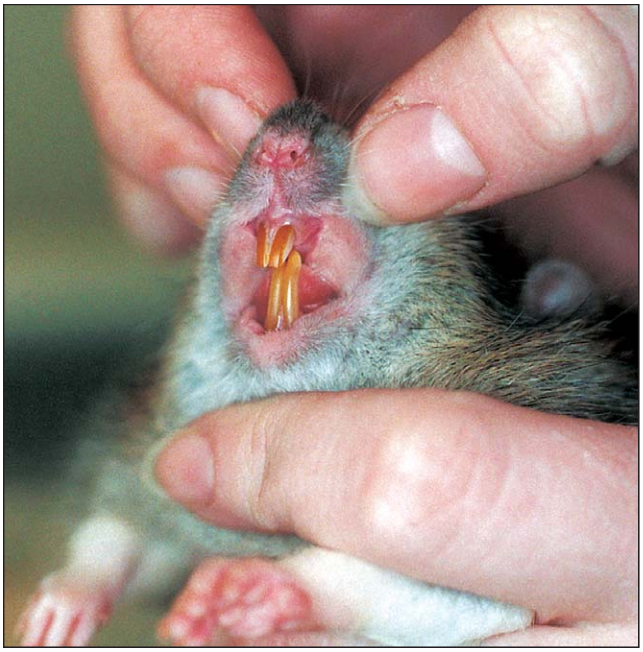


Figure 10.2 • The yellowish color of rat incisors is due to iron pigments. At rest, the lower incisors lie behind the upper incisors and the length of the lower crown is two to three times longer than the upper crown. This is normal and should not be mistaken for malocclusion.

Eyes

The eyes are black, except in albinos. They are spherical in shape and there is frequent blinking. The third eyelid is poorly formed, giving the eyes a bulging appearance (Bivin et al. 1979). Albino rats have poor vision but use sensitive vibrissae and olfaction instead (Harkness & Wagner 1995).

Tail

The tail is long in relation to body size and very sensitive to pain. It plays a large role in thermoregulation and balancing. The cutis of the tail forms over 210 caudally directed overlapping scales, which are heavily keratinized on the upper epidermis (Hebel & Stromberg 1986f). Three short bristles project from each scale. The tail is covered by a layer of orange-yellow sebum.

Feet

There is considerable difference between the length of the front and hindlimbs, enabling the rat to run fast with hopping movements. The rat stands plantigrade so the palmar and plantar skin areas are hairless (they are also devoid of sebaceous glands), with heavily keratinized pads (Hebel & Stromberg 1986e). Sweat glands lie embedded in the fat deposits of the subcutis. These function not for evaporative cooling but for maintaining adhesive friction between the foot and surfaces.

Both fore and hindlimb have five digits, although the first digit of the forefoot is markedly reduced and has a flattened nail (Bivin et al. 1979) (Fig. 10.3). The front paw has five digital pads, three metacarpal and two carpal pads, while the hind leg has five digital, four metatarsal and two tarsal pads (Figs. 10.4 and 10.5). The rest of all the phalanges are covered by a curved claw.

External genitalia

Male

There is a common urogenital aperture (Fig. 10.6). The testicles are evident from 3–4 weeks in the male but the rat may need to be held vertically to let the testes drop into the scrotum. In adult males the large oblong scrotum on either side gives the male rat a rounded distal silhouette. The anus is obscured by the hair but the anogenital distance is twice that of the female. Newborn male rats have a more prominent genital papilla and a greater anogenital distance. There are no nipples in the male.

Female

The female has a shorter anogenital distance than the male. The urethra opens at the base of the clitoris, which is enclosed in a little prepuce. The vulva lies just caudal to this. The female appears to taper towards the tail in a triangular shape (Fig. 10.7).

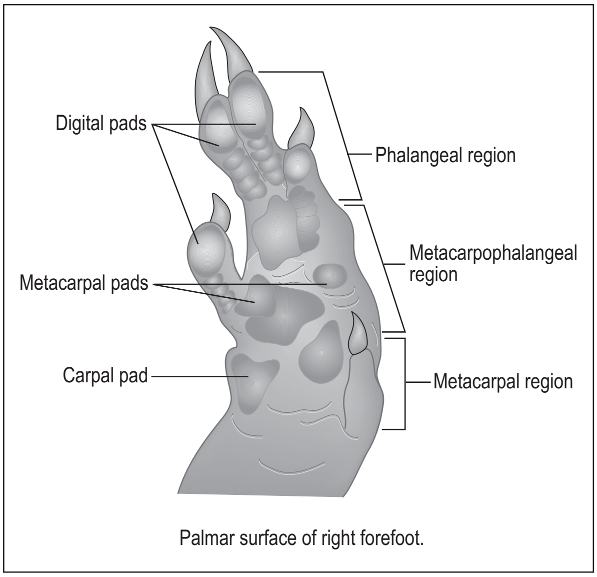

Digital pads
Phalangeal region
Metacarpophalangeal region
Metacarpal pads
Carpal pad
Metacarpal region
Palmar surface of right forefoot.

Figure 10.3 • Palmar surface of right forefoot showing the short first digit.

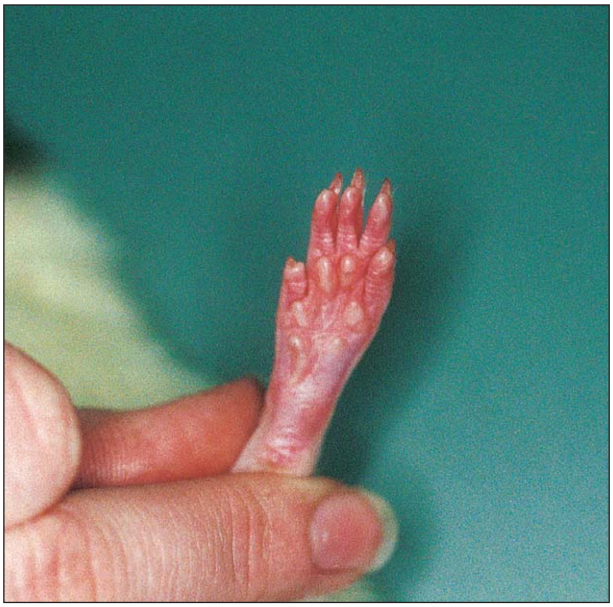


Figure 10.5 • Detail of left hind foot.

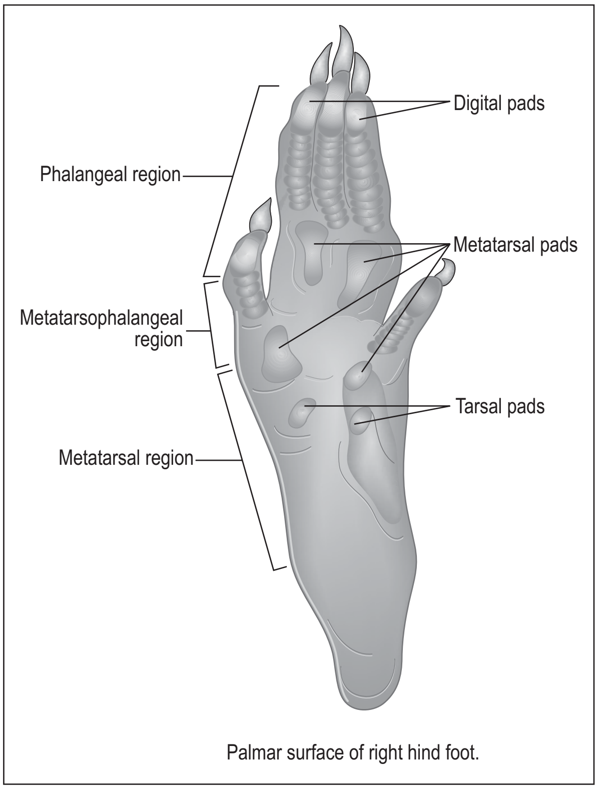

Digital pads
Phalangeal region
Metatarsal pads
Metatarsophalangeal region
Tarsal pads
Metatarsal region
Palmar surface of right hind foot.

Figure 10.4 • Plantar surface of right hind foot.

Mammary glands

There are six mammary glands on each side in the rat: three in the thorax, one in the abdomen and two in the inguinal region. Mammary tissue is extensive, reaching from the neck to the elbow and to the inguinal region. At the axilla a portion even extends dorsally to the shoulder. In the lactating rat they appear to merge as one continuous sheet. Nipples are visible from 8–15 days of age (Fig. 10.22).

SKELETAL SYSTEM

The skeleton of the rat (Fig. 10.8) lacks any unique adaptations to digging, swimming, or running (King & Constance 1982). Along with hamsters and other small rodents, rats lack Haversian systems so ossification is not completed until 1 year of age (much later in relation to puberty than most mammalian species) (Fallon 1996; Percy & Barthold 2001). The proximal humeral epiphysis and distal radius and ulna do not fuse until the end of the 2nd year (Hebel & Stromberg 1986a).

Skull

The skull has a cartilaginous mandibular symphysis and an extremely mobile temperomandibular joint (Hebel & Stromberg 1986a). This, combined with the chisel-like incisors and powerful jaw muscles, makes the rat ideally adapted to the omnivorous state (Figs. 10.9–10.12).

Axial skeleton

There are 7 cervical, 13 thoracic, 6 lumbar, 4 sacral, and 27 to 31 coccygeal vertebrae (Bivin et al. 1979; Hebel & Stromberg 1986a). The sixth cervical vertebrae has a modified rib fused to its transverse processes. Ribs 1–7 articulate with the sternum and the last three are floating ribs. The rat does not have true costal cartilages. The dorsal ribs become ossified first, with the ventral part following later.

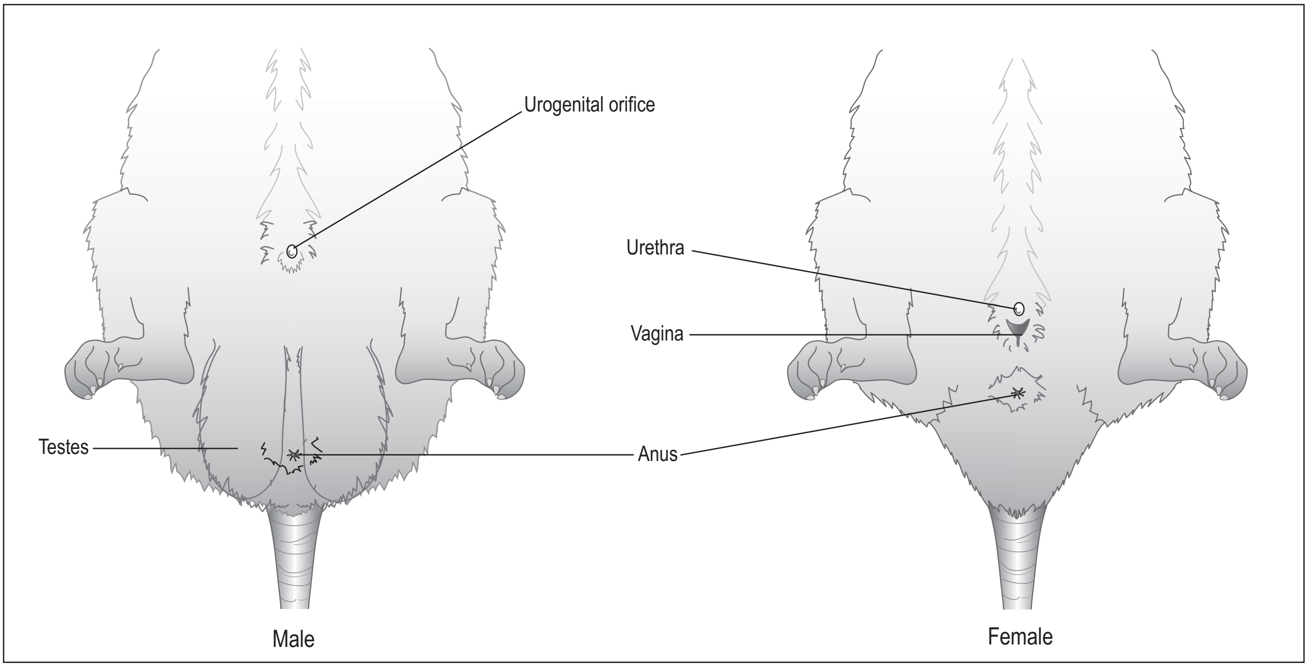


Figure 10.6 • External genitalia.
(a) Male – there is a common urogenital aperture and the anogenital distance is twice that of the female
(b) Female – the urethra and vulva have separate openings and there is a shorter anogenital distance than in the male

Appendicular skeleton

The rat has a well-developed clavicular brace with ligaments similar to the human shoulder joint (Fig. 10.15). A spoon-shaped clavicle articulates with the sternum proximally, and distally with the scapula. The scapula is usually positioned horizontally and has a club-shaped hamate process extending laterally from the scapular spine (Bivin et al. 1979; Hebel & Stromberg 1986a).

The forefeet are well developed and, unlike in the rabbit and guinea pig, have the ability to flex and grasp food in their palms. There are five metacarpal bones: the first digit has two phalanges while the other four all have three phalanges.

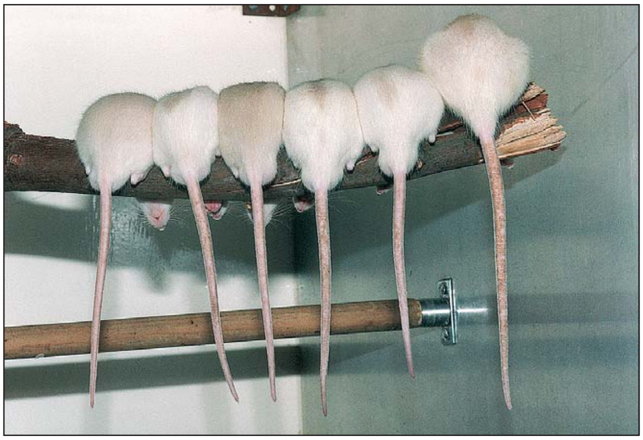


Figure 10.7 • Rats perched on branch showing rounded distal appearance of entire males and triangular appearance of female (*right of picture*). (Photo by Claire Nuttall)

In the young rat the *os acetabulum* fuses with the ischium and ilium to form the acetabulum. The tibia and fibula are fused distally and the tarsus has three rows of bones. The hind feet follow the same pattern as the forefeet but are much better developed (Hebel & Stromberg 1986a).

CARDIOVASCULAR SYSTEM

The pericardium is thin and transparent, with fat deposits at the apex and insertion. It is firmly attached to the thymus cranioventrally. Due to the small size of the left lung the heart is exposed to the thoracic wall on this side (Bivin et al. 1979). There are two cranial vena cavae. The right vena cava empties directly into the right atrium while the left is joined by the azygos vein before joining the caudal vena cava to enter the right atrium (Bivin et al. 1979; Sharp & LaRegina 1998).

The rat has the thinnest pulmonary artery and the thickest pulmonary vein of all rodent species examined. The vein is thicker due to cardiac striated muscle fibers that are continuous with those of the heart and which then extend into the lung tissue. This unfortunately could allow infectious agents to spread from the heart, through the pulmonary veins, and into the lungs (Bivin et al. 1979; Sharp & LaRegina 1998).

Venepuncture sites

The blood volume of the rat is 60 ml/kg and routine blood collection should be limited to 1% of body weight. Blood can be taken from the lateral tail vein, lateral saphenous or ventral tail artery. When intending to sample from the tail it should be warmed well first to cause vasodilation. As the

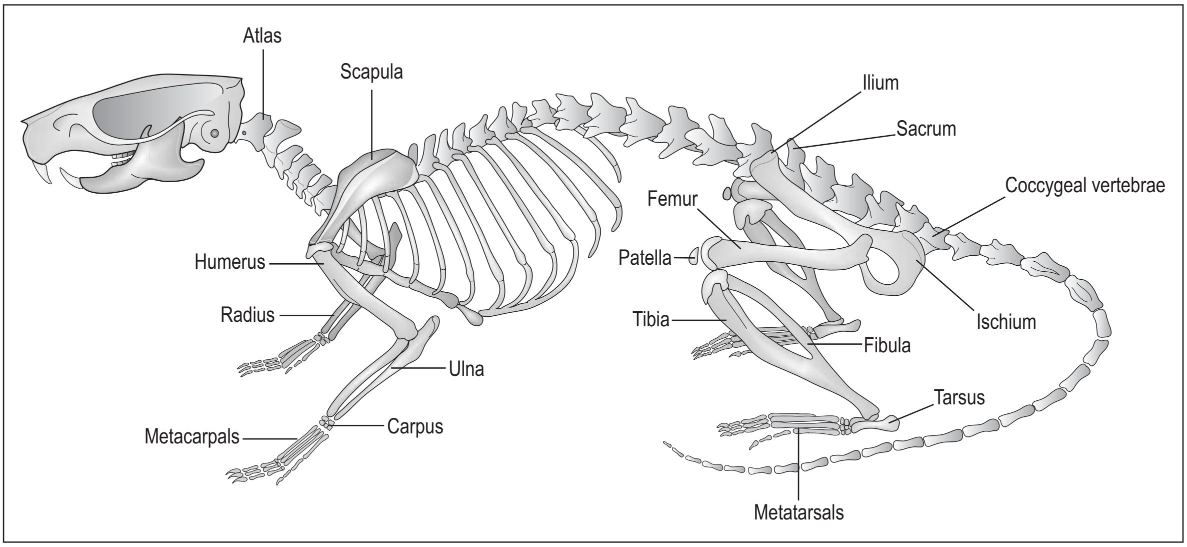


Figure 10.8 • Skeleton of Brown rat (*Rattus norvegicus*). From Popesko, P., Rajtova, V., & Horak, J. (1990) A colour atlas of anatomy of small laboratory animals. Vol. 2. Aylesbury, UK: Wolfe with permission.

ventral tail artery has high blood pressure no syringe plunger is necessary, although good hemostasis is required after removal of the needle to avoid excessive blood loss (Fallon 1996).

IMMUNE SYSTEM

The lymphatic vessels and lymph nodes are similar to those in most mammals. The mesenteric lymph node is the largest lymph node and is often embedded in fat in obese rats.

Thymus

Most of the thymus lies in the cranial mediastinum, with a small cervical part lying ventral to the trachea. Like all rodents it persists into adult life (Bivin et al. 1979; Percy & Barthold 2001).

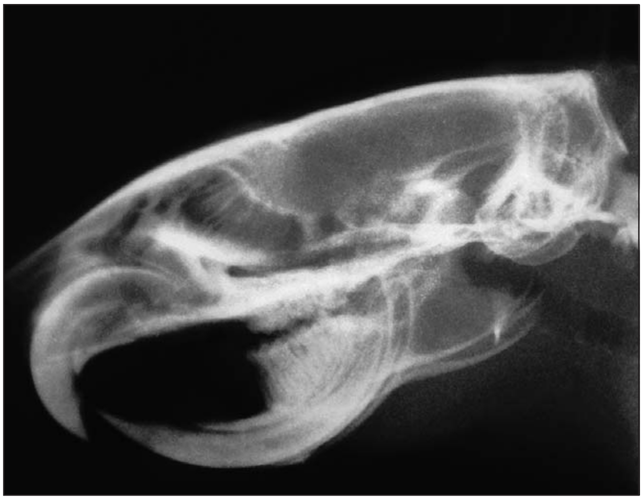


Figure 10.9 • Lateral radiograph of rat skull.

Spleen

The spleen lies in the left dorsal cavity between two layers of omentum. It is oblong in shape and larger in males than in females. It is a major site of red cell breakdown (Bivin et al. 1979).

RESPIRATORY SYSTEM

The nasal cavity is involved not only with respiration but with humidifying and filtering incoming air. As in all rodents, it also plays a major role in olfaction. Over 50% of the nasal cavity is lined by olfactory epithelium, giving rats their acute sense of smell. In contrast, man has only 3% of the nasal cavity lined by olfactory epithelium (Harkema & Morgan 1996). The vomeronasal organ, which lies about 10 mm from the vestibule in the ventral vomer bone, also plays a role in olfaction (Harkema & Morgan 1996; Hebel & Stromberg 1986d).

The length of the trachea from first cartilage to bifurcation is 33 mm. It is a flattened oval in cross-section and is 3×2 mm wide (Hebel & Stromberg 1986d). The right lung has a cranial, middle, caudal, and accessory lobe. The left lung is smaller and not divided into lobes. Due to its small size the heart is quite accessible on the left side, so cardiac puncture could be achieved between ribs 3 and 5 (Figs. 10.14 and 10.15).

Steno's gland

The rat has several well-developed nasal glands but the largest is Steno's gland. This lies in the rostral maxillary sinus and its duct empties at the vestibule. This gland is homologous with the salt gland of marine birds. It produces a watery secretion at the nose where it may help to humidify inspired air and regulate mucus viscosity (Bivin et al. 1979; Sharp & LaRegina 1998).

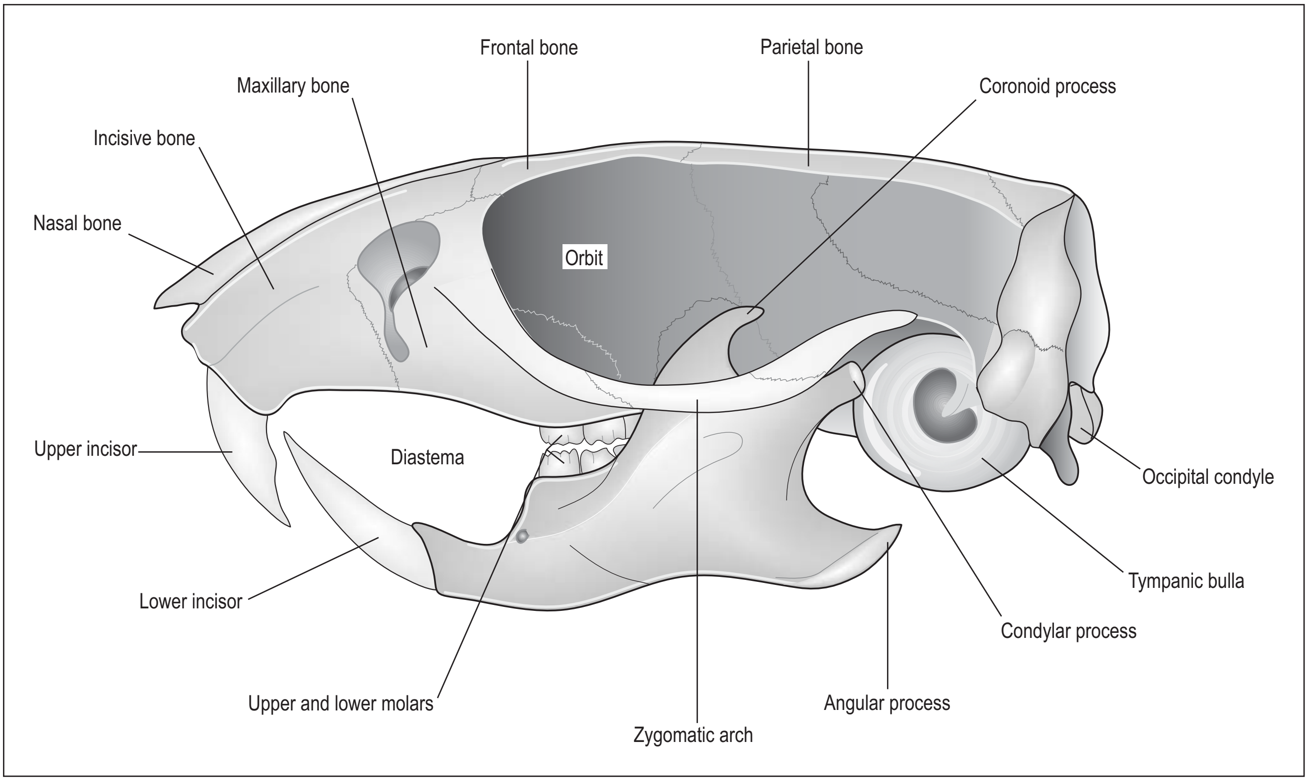


Figure 10.10 • Lateral view of rat skull. From Popesko, P., Rajtova, V., & Horak, J. (1990) A colour atlas of anatomy of small laboratory animals. Vol. 2. Aylesbury, UK: Wolfe with permission.

DIGESTIVE SYSTEM

Rats are omnivores and feed frequently. Food is grasped in the forepaws, chipped by the incisors, and ground down by the molars. Gastrointestinal transit time varies from 12 to 24 hours. Food restriction, as opposed to ad lib feeding, has been found to increase longevity and decrease incidence of tumors in ageing rats (Koolhaas 1999; Yu 1994).

Oral cavity

The tongue is about 30 mm long and 8 mm wide from rostral tip to epiglottis (Fig. 10.13). It is compressed in the middle to allow space for the molar teeth. The dorsal surface has a caudal prominence called the *lingual torus*, which has abundant gustatory and mechanical papillae (Bivin et al. 1979; Hebel & Stromberg 1986c).

There are no tonsils. The hard palate has prominent ridges and is distinguished from the soft palate by a pale line in the mucous membrane (Bivin et al. 1979). Taste buds are found throughout the oral cavity from the dorsal tongue, along the rostral edge of the soft palate, and on the hard palate.

Dentition

There are 16 teeth and the dental formula is 1/1,0/0,0/0,3/3. The cheek tissue can be drawn into the diastema, closing off the back of the mouth to allow the rat to gnaw on hard substances without having debris pass into the pharynx (Bivin et al. 1979).

Incisors

As is the case with all rodents, the incisive bone is well developed. The incisors erupt about 10 days after birth, the molars on day 19 and all teeth are in wear by 6 weeks. Rats are monophyodont, meaning they only produce one set of teeth (Hebel & Stromberg 1986a; Schour & Massler).

The incisors are open rooted (aradicular) and constantly growing so need to be worn down by gnawing. The incisors grow in the shape of a spiral, the upper incisors being more tightly curved than the lower (Fig. 10.16). The ability of the temperomandibular joint to allow cranial and caudal jaw movement keeps the tips sharp by gnawing. The lingual side has softer dentine so wears down faster, creating the appearance of the bevel of a hypodermic needle. The incisors have a yellow-orange color due to the presence of iron pigments and this deepens with age (Schour & Massler).

CLINICAL NOTE

At rest, the lower incisors lie behind the upper incisors and the length of the lower crown is three times as long as the upper crown. This is normal and should not be mistaken for malocclusion (Fig. 10.2).

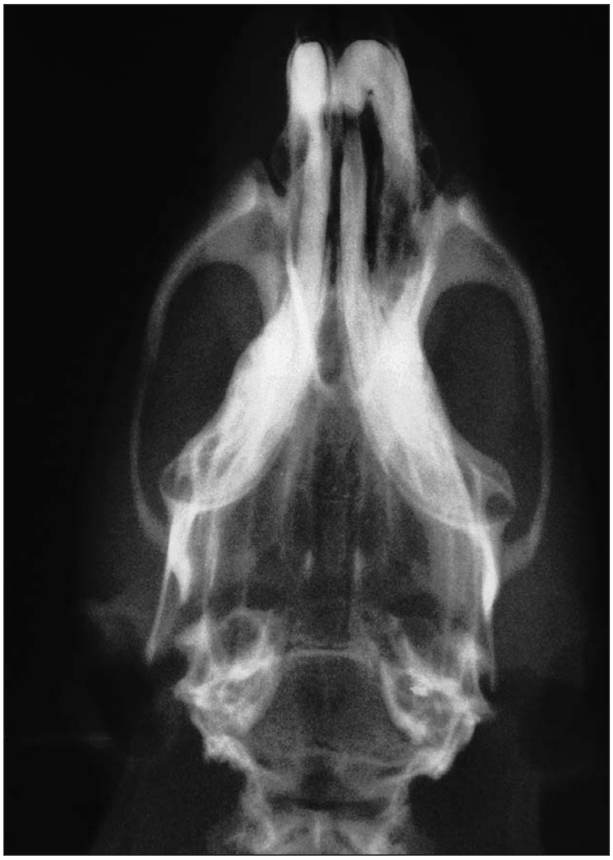


Figure 10.11 • Dorsal radiograph of rat skull.

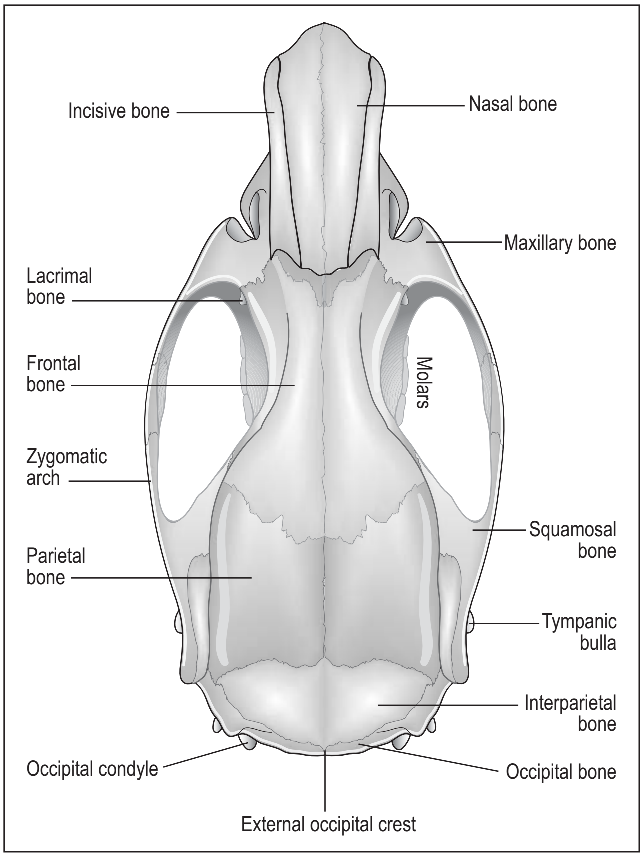


Figure 10.12 • Dorsal view of rat skull.

The rate of eruption is balanced by the rate of attrition so the length of the teeth remains constant. When a tooth is fractured or maloccluded the eruptive forces increase 2–3 times, causing rapid elongation of the tooth. The teeth usually grow in a spiral fashion, often perforating the lips (Schour & Massler).

Molars

These provide the grinding action on the food. They are closed rooted (brachiodontic) and stop growing at about 125 days after birth. The size of the molars decreases from M1 to M3 (Hebel & Stromberg 1986a). The masticatory surface has transversely orientated enamel folds with nine enamel-free cusps arranged in three rows of three. The upper and lower jaws are of equal width but only one side will be in apposition at a time during chewing.

Muscles of mastication

Rats, like all myomorphs, have a well-developed zygomatic arch and strong jaw muscles (Fig. 10.17). The masseter, temporalis, and pterygoideus close the jaw; the digastricus opens the mouth and draws the mandible backward (Hebel & Stromberg 1986b).

The masseter muscle (medial and lateral) is the most powerful and extends from the lateral zygomatic arch to the mandible. In all myomorphs a slip of the medial masseter runs through the infraorbital canal to insert on the muzzle. This gives a strong cranial pull on the lower jaw and aids grinding and gnawing (King & Custance 1982). The temporalis muscle originates from the temporal fossa and inserts on the coronoid process and medial mandible. The pterygoideus muscle extends from pterygoid/palatine bone and inserts on condyloid and medial angular process. The digastricus muscle, which opens the mouth, arises from the occipital bone and inserts just caudal to the mandibular symphysis (Hebel & Stromberg 1986b).

Salivary glands

These consist of the greater salivary glands (parotid, mandibular, and greater sublingual) and the minor salivary glands (sublingual, buccal, palatine, and lingual). The parotid gland is quite diffuse and extends from behind the ear almost to the shoulder (Sharp & LaRegina 1998). The mandibular salivary gland lies in the ventral cervical region about 10 mm rostral to the thoracic inlet (head extended). It borders the mandibular lymph node rostrally. The greater sublingual gland is also tightly attached to this gland rostrally (Bivin et al. 1979; Hebel & Stromberg 1986c).

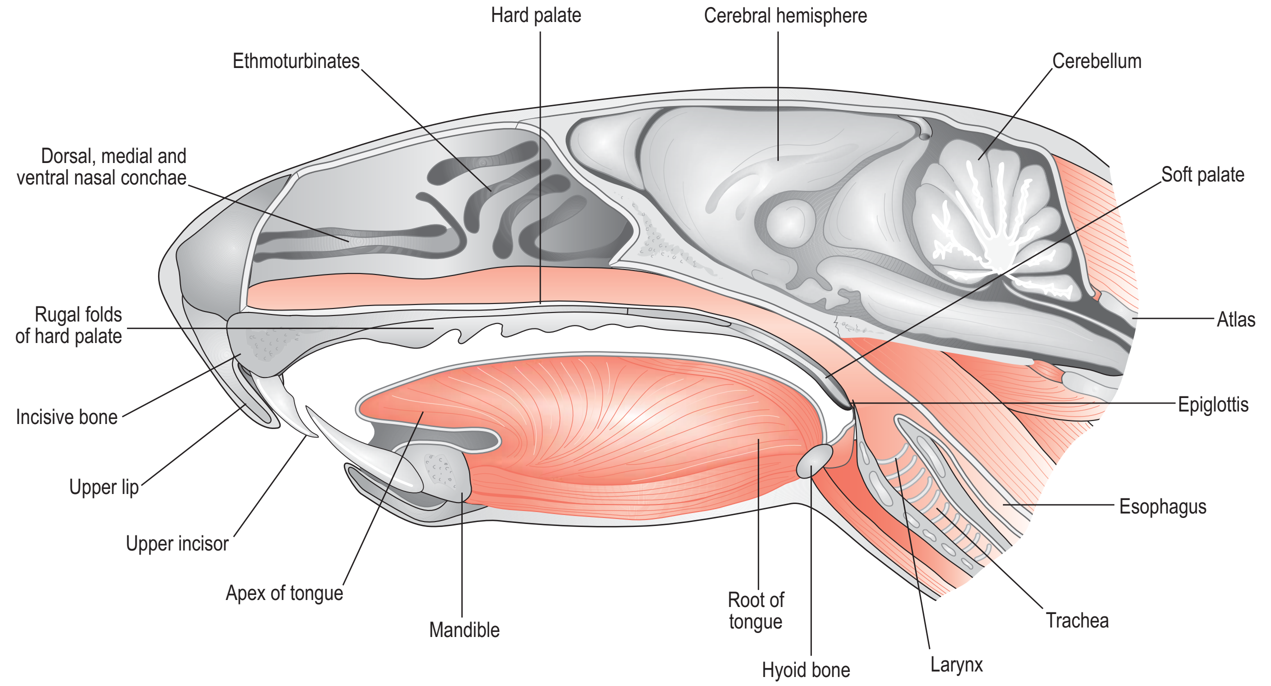

Hard palate
Cerebral hemisphere
Ethmoturbinates
Cerebellum
Dorsal, medial and ventral nasal conchae
Soft palate
Rugal folds of hard palate
Atlas
Epiglottis
Incisive bone
Upper lip
Esophagus
Upper incisor
Apex of tongue
Mandible
Root of tongue
Trachea
Hyoid bone
Larynx

Figure 10.13 • Midsaggital view through head of rat. The larynx is placed high in the oropharynx where it can directly access the nasopharynx, making rats and rodents obligate nose breathers. From Popesko, P., Rajtova, V., & Horak, J. (1990) A colour atlas of anatomy of small laboratory animals. Vol. 2. Aylesbury, UK: Wolfe with permission.

The salivary glands and lymph nodes in the ventral cervical region are covered by extensive areas of brown fat, which extends from the mandible to the axilla and should not be confused with lymph nodes or glands (Greene 1962).

CLINICAL NOTE

Rats can get Sialodacryoadenitis virus (SDAV) which causes inflammation and edema of the cervical salivary glands and lymph nodes, creating the appearance of mumps. SDAV is highly contagious and usually self-limiting, although affected rats pose an anesthetic risk due to enlarged glands pressing on the respiratory tract (Fallon 1996).

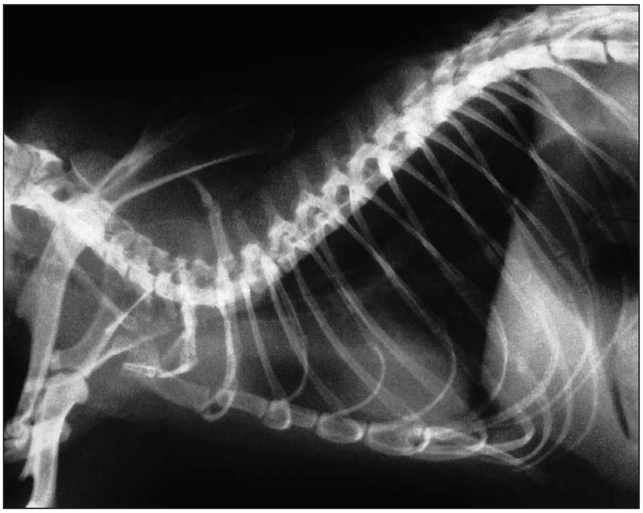


Figure 10.14 • Lateral radiograph of thorax.

Esophagus and stomach

The abdominal muscles and linea alba are very thin. The esophagus runs slightly to the left in the cervical region and then along the dorsal midline. It has a diameter of approximately 2 mm and has skeletal muscle along its length. The esophagus enters the stomach in the middle of the lesser curvature. A limiting ridge at this junction prevents rats from vomiting (Bivin et al. 1979).

The stomach lies transversely, caudal to the rib cage on the left side with its parietal surface covered by the left liver lobe. A lobulated cushion of fat (which is embedded in the mesorchium or mesovarium) is sandwiched between the stomach and the abdominal wall. The oblong spleen is also in contact with the greater curvature.

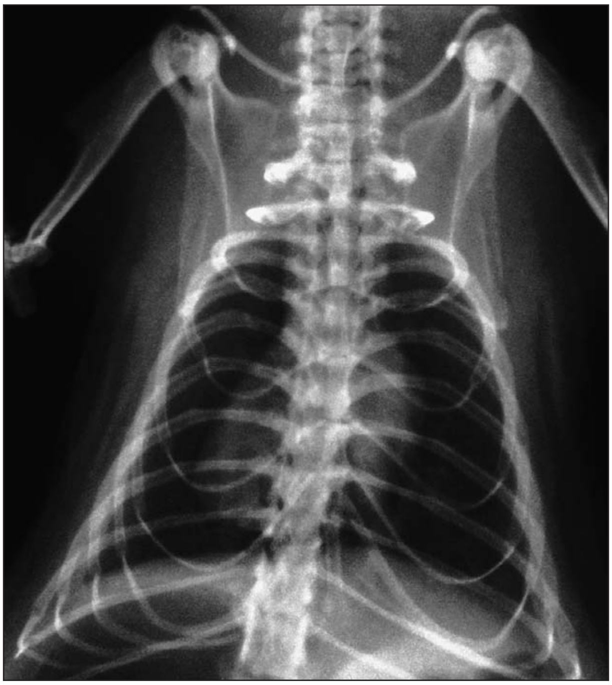


Figure 10.15 • Ventrodorsal view of thorax in rat. Note the well-developed clavicular brace.

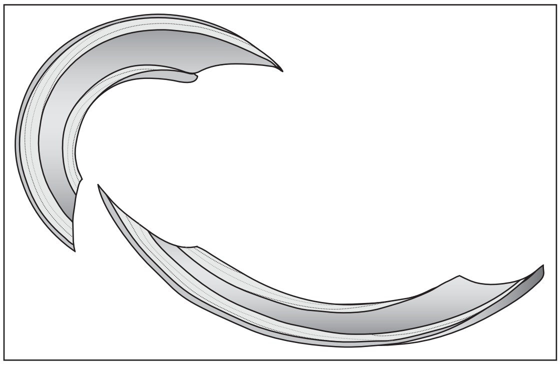
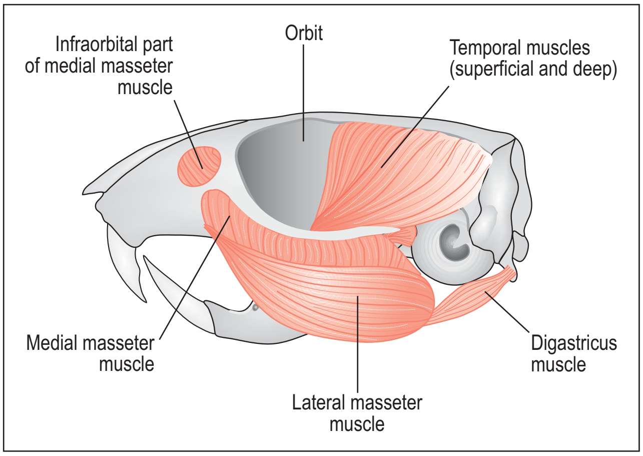


Figure 10.16 • The correct alignment of incisor teeth in the adult rat. The lower incisors lie behind the upper at rest and the ends should be sharp like a chisel.

The stomach is monogastric and divided into two parts by a limiting ridge (Fig. 10.18). There is the non-glandular forestomach, which like the esophagus is lined by thicker stratified squamous epithelium. In the distal glandular part the mucosa is occupied by fundic glands containing chief and parietal cells. There is a heavily muscled pyloric sphincter. The omentum is moderately developed and separates the jejunum and cecum from the visceral face of the stomach (Hebel & Stromberg 1986c).

Small intestine

The short intestine is approximately 113 cm in length. The jejunum is the longest part (~100 cm) and fills the right ventral abdomen. It has a long mesentery which allows the jejunal loops to spread to all parts. The opening of the ileum into the cecum lies close to the opening of the colon (Komarek et al 2000)(Figs. 10.19 and 10.20).



Infraorbital part of medial masseter muscle
Orbit
Temporal muscles (superficial and deep)
Medial masseter muscle
Digastricus muscle
Lateral masseter muscle

Figure 10.17 • Muscles of mastication in the rat.
Note the powerful masseter muscle (medial and lateral), which extends from the lateral zygomatic arch to the mandible. From Popesko, P., Rajtova, V., & Horak, J. (1990) A colour atlas of anatomy of small laboratory animals. Vol. 2. Aylesbury, UK: Wolfe with permission.

Large intestine

The comma-shaped cecum commonly lies in the left caudal abdomen, although its long mesentery means its position varies quite considerably (Hebel & Stromberg 1986c; Komarek et al. 2000b). Although it has no septa dividing it, as seen in other rodents, it can be divided into base, body, and apex (Sharp & LaRegina 1998). The body lies along the left lateral wall. Its layers are much thinner than the other parts of the intestine and lymphoid tissue is found near the apex, corresponding to the appendix.

The colon is divided into ascending, transverse, and descending. The proximal colon is similar to the cecum but it becomes thicker distally. At the end of the rectum a zone between the skin and the glandular mucous membrane contains numerous sebaceous glands, which could be called anal glands.

Liver

The liver lies in close contact with the rib cage. There are four lobes: the left lateral, left medial, middle, and right lobe. The visceral surface contacts the stomach, descending duodenum, transverse colon, jejunum, and spleen. Rats have no gall bladder (Bivin et al. 1979). The bile ducts unite to form the hepatic duct, which runs through the pancreas. Bile and pancreatic juices then enter via a common duct into the proximal duodenum near the pylorus (Hebel & Stromberg 1986c; Komarek 2000).

Pancreas

The pancreas is whitish gray, heavily lobulated and very diffuse. It can be distinguished from adipose tissue by its

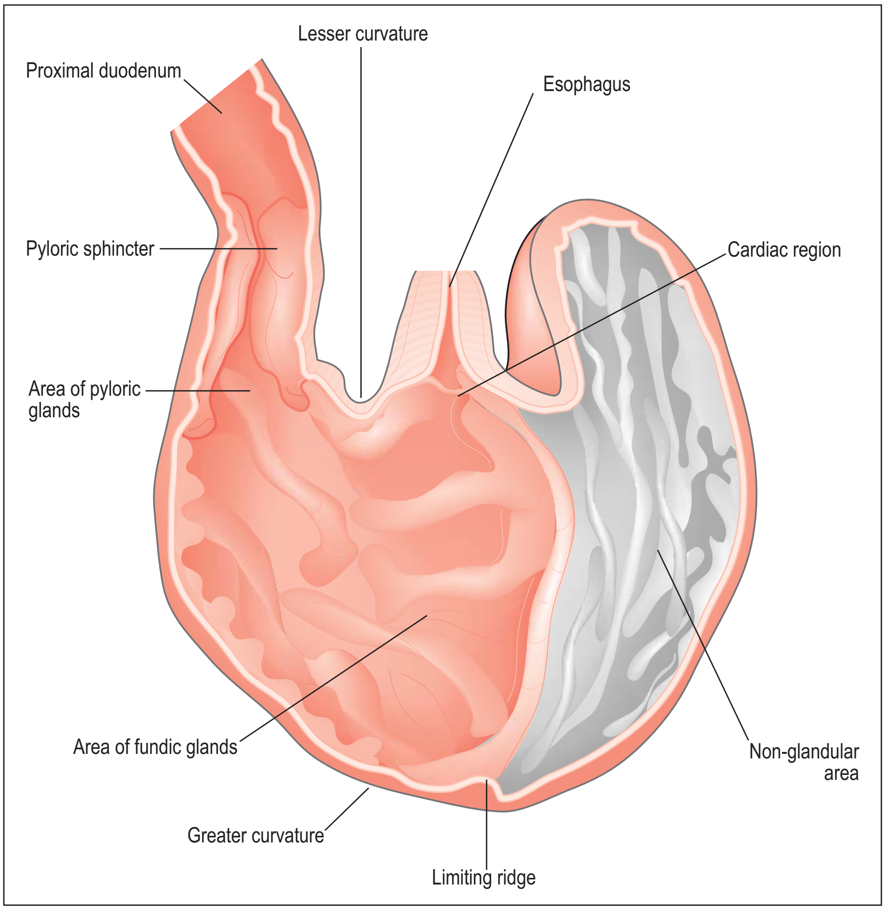

Proximal duodenum
Lesser curvature
Esophagus
Pyloric sphincter
Cardiac region
Area of pyloric glands
Area of fundic glands
Non-glandular area
Greater curvature
Limiting ridge

Figure 10.18 • Internal cross-section of rat stomach showing limiting ridge which divides glandular from non-glandular tissue.

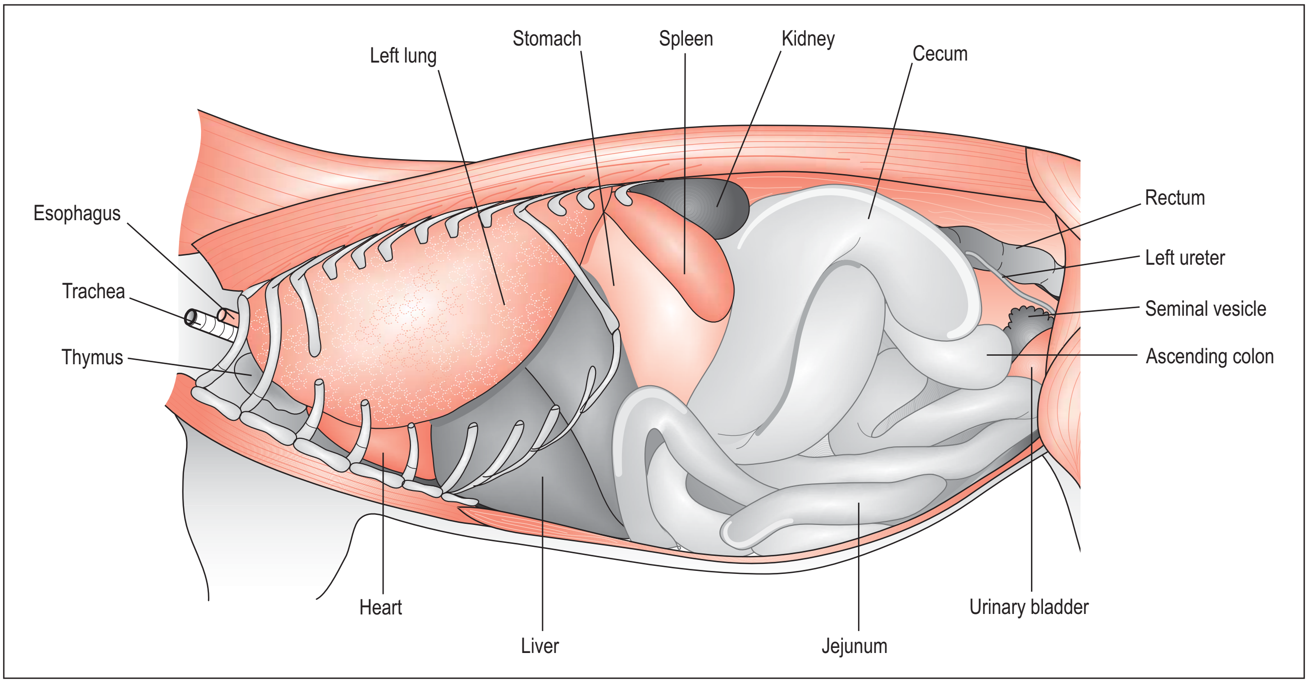

Left lung
Stomach
Spleen
Kidney
Cecum
Esophagus
Rectum
Trachea
Left ureter
Seminal vesicle
Thymus
Ascending colon
Heart
Liver
Jejunum
Urinary bladder

Figure 10.19 • Right lateral thorax and abdomen (some ribs removed). From Popesko, P., Rajtova, V., & Horak, J. (1990) A colour atlas of anatomy of small laboratory animals. Vol. 2. Aylesbury, UK: Wolfe with permission.

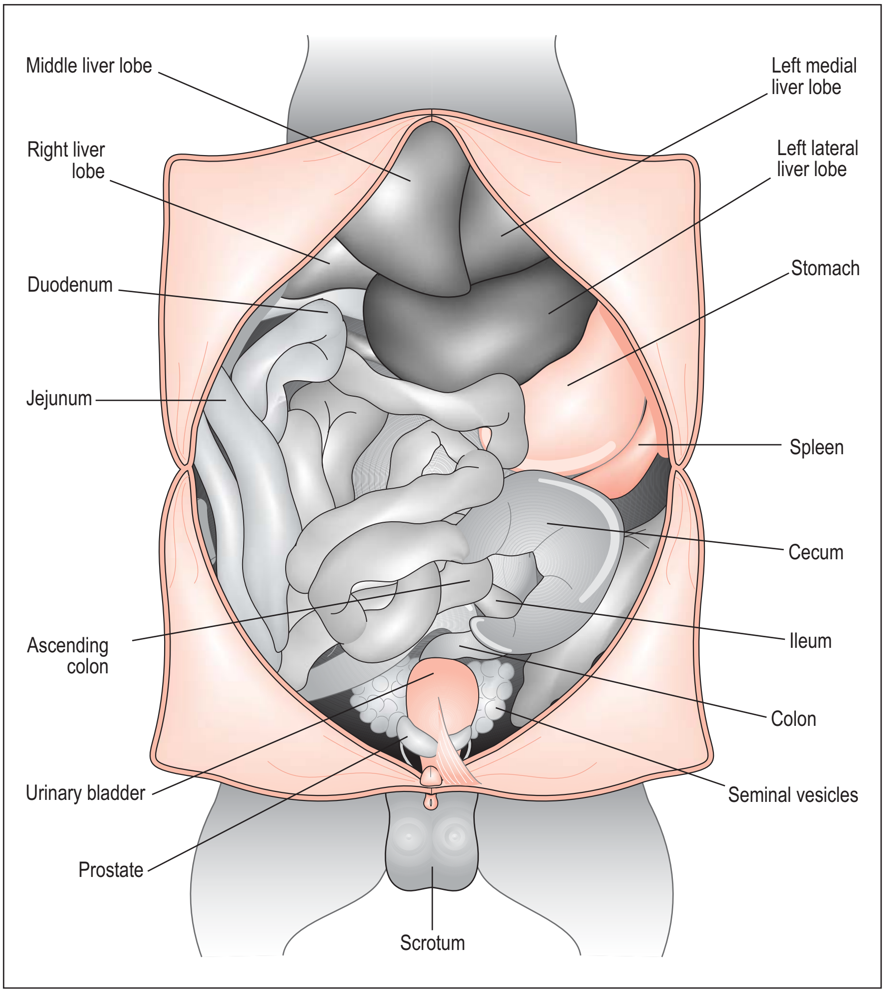


Figure 10.20 • Ventral abdomen of male rat. The cecum of the rat has a very long mesentery so the location can vary. From Popesko, P., Rajtova, V., & Horak, J. (1990) A colour atlas of anatomy of small laboratory animals. Vol. 2. Aylesbury, UK: Wolfe with permission.

darker color and firmer consistency (Hebel & Stromberg 1986c; Sharp & LaRegina 1998).

URINARY SYSTEM

The kidneys are bean shaped and reddish brown. The right kidney lies at the level of L1–L3, with the left kidney lying slightly caudal to the right. Both lie equidistant from the midline with their long axis converging cranially. In healthy rats adipose tissue surrounds the hilus and sides. Like other rodents, the kidney is unipapillate and has one papilla and one calyx entering the ureter directly (Bivin et al. 1979; Hebel & Stromberg 1986g; Sharp & LaRegina 1998). The presence of more long loop nephrons gives the rat an excellent ability to concentrate its urine (28% in comparison to 14% in man) (Bivin et al. 1979).

The urinary bladder lies cranial to the rim of the pubis. It is pear shaped when empty and spherical when full, stretching to 25×15 mm or more. In the male, the ventral lobe of the prostate gland attaches to the ventrolateral wall of the bladder and the urethra extends through the penis. In the female the urinary and reproductive openings are totally separate (Hebel & Stromberg 1986g).

Urine output is approximately 15–30 ml daily and proteinuria can be a normal finding (Bivin et al. 1979). Unlike the rabbit, the rat excretes only small quantities of calcium in the urine, even when fed a calcium rich diet (Cheeke & Amber 1973).

REPRODUCTIVE SYSTEM

Male

In adults the scrotum is easily visible ventrolateral to the anus. The skin of the scrotum is thin and covered with fine hairs. The inguinal canal remains open throughout life and has a distended diameter of 8–12 mm, which allows the testis to have a scrotal or inguinal position. The testes descend between 30–40 days (Bivin et al. 1979; Greene 1962; Hebel & Stromberg 1986g).

The testis is oval in shape and measures 20×14 mm. The head and tail of the epididymis are often sites of extremely large fat pads. The penis can easily be extruded from the prepuce and has an os penis (Hebel & Stromberg 1986g).

Accessory genital glands

Male rats have highly developed accessory sex glands (Bivin et al. 1979; Hebel & Stromberg 1986g) (Fig. 10.21). These produce a gelatinous copulatory plug, which is visible in the vagina post mating and is thought to prevent semen leaking out.

- Seminal vesicles – These lie dorsolateral to the urinary bladder and are in contact with the rectum dorsally. They are large and lobulated, opening into the lower end of the vas deferens. Each is enclosed in a capsule together with the coagulating gland.
- Prostate gland – This is bilateral and has three lobes: the dorsal, the lateral, and the ventral. The dorsal lobe, also known as the coagulating gland, lies close to the seminal vesicles (Komarek et al. 2000b).
- Ampullary glands – These are the glands of the ductus deferens and lie near the bladder.
- Bulbourethral glands – These are found near the urethra as it exits the pelvis.

Preputial glands

Preputial glands lie in the subcutaneous fat near the penis and open into the prepuce. These are sebaceous glands that secrete a pheromone used for scent marking. These regress with ageing and the glands can fill up with stagnant sebum. An analogue is also present in the female (Hebel & Stromberg 1986g; Komarek et al. 2000b).

Female

The right ovary is located at the level of L4–5 just caudal to the right kidney. The left ovary lies at L5–6 caudal to the left kidney. The left ovary is nearer the midline than the right. Both are embedded in fat (Bivin et al. 1979; Hebel & Stromberg 1986g). The oviduct is convoluted and winds around the ovary in 10 to 12 garland-like loops. The uterus is duplex, meaning the two parts are separate along its entire length, uniting only at the vagina (Greene 1962; Hebel & Stromberg 1986g; King & Custance 1982). There is partial fusion caudally for 7–10 mm where they share the outer longitudinal layer of myometrium. Like most mammals an anastomosis between the ovarian artery (a branch of the aorta) and the uterine artery (a branch of the internal iliac) occurs in the uterine mesentery (Del Campo & Ginther 1972).

The mesovarium and mesometrium contain voluminous amounts of fat, which surrounds the kidneys, abdominal

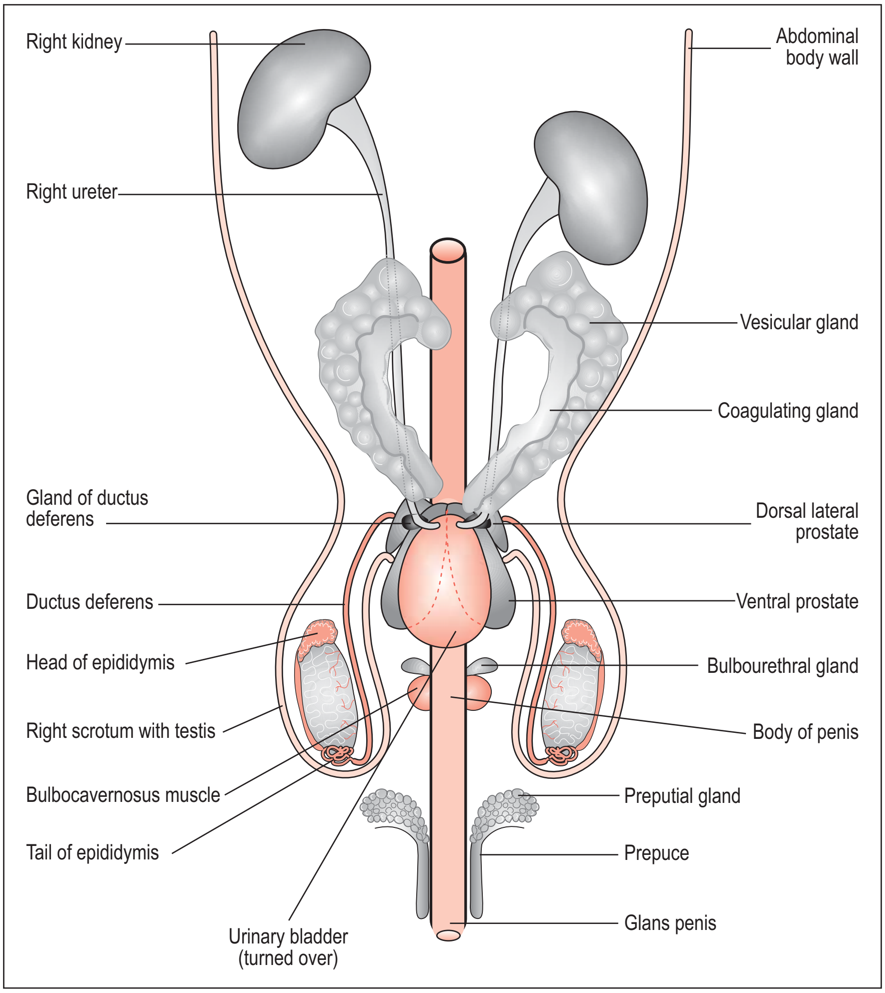

Right kidney
Abdominal body wall
Right ureter
Vesicular gland
Coagulating gland
Gland of ductus deferens
Dorsal lateral prostate
Ductus deferens
Ventral prostate
Head of epididymis
Bulbourethral gland
Right scrotum with testis
Body of penis
Bulbocavernosus muscle
Preputial gland
Tail of epididymis
Prepuce
Glans penis
Urinary bladder (turned over)

Figure 10.21 • Ventral view of male genital tract showing the extensive accessory glands.

wall, and intestinal loops. There are no vaginal glands. In the female rat the urethra and vaginal orifice are completely separate. The only genital structure connected with the urinary system is the clitoris. The urethra lies cranially at the base of the clitoris and both are located in a high cone with clitoral glands. The vaginal opening lies caudal to this and is closed by a membrane until puberty in the female. The female has six pairs of mammary glands (Bivin et al. 1979; Hebel & Stromberg 1986g).

Clitoral (preputial) glands

These paired glands lie in the subcutaneous fat near the clitoris and open into a preputial fold. These are sebaceous glands that secrete a pheromone used for scent marking (Komarek et al. 2000b).

Mammary glands

The glandular tissue changes volume and appearance during the estrous cycle, pregnancy, and lactation. Prior to the first pregnancy these glands consist of a few short tubules around the teats but these expand into each gland before parturition.

The cervical gland is rudimentary whereas the thoracic gland is diffuse, contains three nipples, and surrounds the base of the forelimb. The abdominal gland is only marginally developed while the inguinal gland has three nipples and surrounds the base of the hindlimbs (Komarek 2000). The thoracic and inguinal glands act as two discrete complexes, separated by a space just behind the ribs (Fig. 10.22). During lactation the thoracic glands expand rostrally as far as the parotid and mandibular glands, cranially and medially over the upper arm, and along the lateral thoracic wall. Caudally, the inguinal gland covers the lateral abdominal wall right back to the stifle and the anal region (Hebel & Stromberg 1986e; Komarek et al 2000b; Maeda et al. 2000).

At the base of each teat the transition zone between hairless and hair has large sebaceous glands. There are no teats in the male although mammary tissue can still be found in the corresponding area (Hebel & Stromberg 1986e).

Reproductive physiology

Photoperiod has a strong influence on the hypothalamus, which means it also affects the estrous cycle. The luteinizing hormone (LH) surge is strongly linked to the circadian rhythm and usually occurs in the late afternoon. Stress and suckling suppresses LH secretion and, hence, ovulation (Maeda et al. 2000).

Estrous cycle

Females are polyestrous, with a 4–5 day estrus. Ovulation occurs 9–10 hours after the commencement of estrus. Vaginal

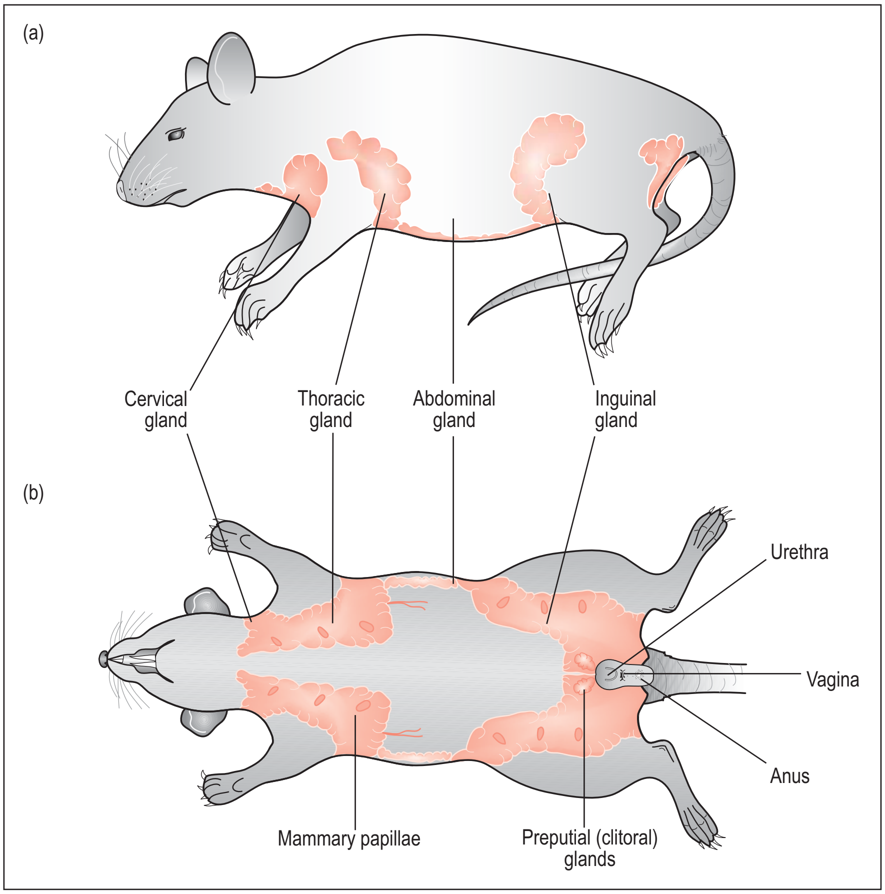


Figure 10.22 • Mammary tissue of the female rat is extensive, reaching from the neck and elbow to the inguinal region. There are six mammary glands on each side in the rat – three in the thorax, 1 abdominal, and two in the inguinal region.
(a) Lateral view of mammary glands
(b) Ventral view of mammary glands
From Popesko, P., Rajtova, V., & Horak, J. (1990) A colour atlas of anatomy of small laboratory animals. Vol. 2. Aylesbury, UK: Wolfe with permission.

CLINICAL NOTE

Mammary tumors are common in rats, and due to the extensive distribution of the mammary tissue, can appear anywhere from the axilla to the groin. They can occur in both males (16%) and females and incidence increases at over 18 months of age (Altman & Goodman 1979). About 80 to 90% are benign fibroadenomas (Percy & Barthold 2001) so surgical removal is recommended (Figs. 10.23 and 10.24). They can be associated frequently with pituitary tumors (Altman & Goodman 1979).

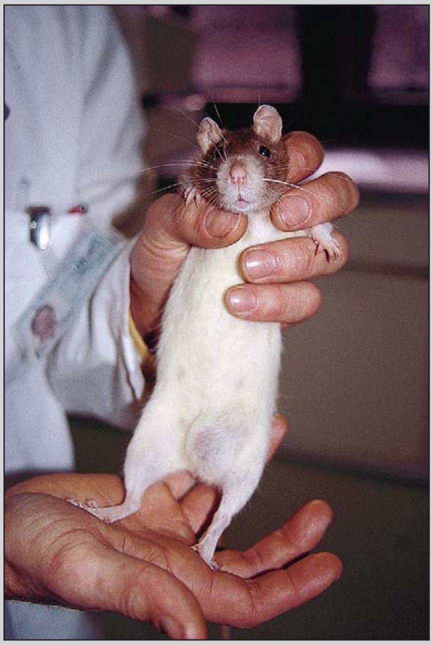


Figure 10.23 • Female rat with large tumor of inguinal mammary gland.

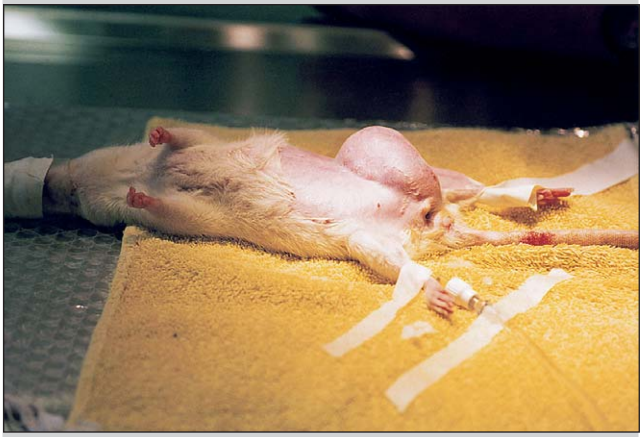


Figure 10.24 • Rat undergoing surgery to remove large inguinal tumor. Histopathology revealed a benign fibroadenoma.

smears can be used to identify the phase of the cycle as estrogen causes a proliferation of vaginal epithelial cells during proestrus (Harkness & Wagner 1995) (Table 10.1).

Gestation

The gestation period is 21–23 days. The rat has a hemochorial placenta. There is little change in the uterus in the first trimester but after this it moves ventrally, displacing intestinal coils cranially. Parturition is usually by day and is quick, taking about 90 minutes to produce a litter which can vary in size from 3 to 18 (Maeda et al. 2000).

Birth

The pups weigh 5–6 g at birth and are altricial, with closed ears and eyes (Harkness & Wagner 1995). They have no intrinsic thermoregulatory mechanisms until the end of the first week of life so are kept warm by siblings and the mother (Fallon 1996; Koolhaas 1999). The ears open within 4 days and eyes open by the end of the 2nd week. Full hair has grown by the 7–10th day (Baker 1979; Fallon 1996; Koolhaas 1999).

ENDOCRINE ORGANS

Pituitary gland

This reddish-brown organ is located in a bony cavity, the sella turcica, ventral to the diencephalon, and caudal to the optic chiasma.

CLINICAL NOTE

Tumors of the pituitary glands are extremely common in ageing rats, with more females than males being affected (Altman & Goodman 1979; Percy & Barthold 2001).

Thyroid gland

The thyroid lobes lie ventrolateral to the first 4 to 5 tracheal rings and consists of two pinkish lobes connected by a delicate isthmus (Komarek et al 2000).

Parathyroid

The rat has only one pair of parathyroid glands, which usually lie at the cranial aspect of the thyroid gland. They are circular and paler in color.

Adrenal glands

These are brown and beanlike and lie in the retroperitoneal fat close to the cranial pole of each kidney and attached to

Table 10.1 Interpretation of vaginal smears in the rat (Sharp 1998; Baker 1979)

Phase of cycle	Length (hours)	Vaginal cytology	Presence of Leukocytes
Proestrus	12	Nucleated epithelial cells	Small number
Estrus	12	Cornified cells, no nuclei	Small number
Metestrus	21	Cornified epithelial cells	Large numbers
Diestrus	57	Few epithelial cells	Large numbers

the ventral sublumbar muscles. The right adrenal is covered by the caudate lobe of the liver. The left adrenal lies nearer to the midline than the right. The adrenal gland is larger in the female than the male. Wild rats also have larger adrenals than domesticated laboratory rats (Bivin et al. 1979; Percy & Barthold 2001).

SENSES

The rat, being mainly nocturnal, has a well-developed sense of hearing, touch, and smell, but vision is poor (Sharp & LaRegina 1998). Albinos have especially poor eyesight due to retinal degeneration.

Sight

The eyes are small and placed laterally. Although it can see through 360 degrees the rat has a blind spot in front of its nose. The cornea is large and the large lens is round, with little power of accommodation. The retina is rod dominated (as would be expected in nocturnal species) and holangiotic, with radial vessels and a centrally located optic disk. Although the rat does not move its eye, the ocular muscles are quite well developed. Unlike other rodents, a venous orbital sinus is not developed but there is a venous plexus formed by the anastomoses of the dorsal and ventral ophthalmic veins (Hebel & Stromberg 1986f).

Eyelids

The palpebral fissure opens between the 14th and 17th days after birth. The eyelids are covered by hair. Two lacrimal ducts open at the puncta located at the medial canthus of the eye and these join to form the 22 mm long nasolacrimal duct, which opens just caudal to the nostril in the vestibule (Hebel & Stromberg 1986f).

Harderian gland

This conical, red-brown gland lies behind the eye and fills a large part of the orbit. It is larger than the eye itself and its excretory ducts fuse to form one single duct that empties into the medial canthus of the eye behind the nictitating membrane (Bivin et al. 1979; Komarek et al 2000b). This gland secretes lipids and a porphyrin red pigment which fluoresces under ultraviolet light. These secretions play a role in ocular lubrication and pheromone behavior and are spread over the skin during grooming. This hypersecretes when the rat is stressed, creating a red-brown deposit around the eyes and nose known as *chromodacryorrhea* (Harkness & Wagner 1995; Hebel & Stromberg 1986f) (Fig. 10.25).

Lacrimal gland

The rats has two pairs of lacrimal glands: the extraorbital and the infraorbital. The extraorbital is located at the base of the ear, rostrodorsal to the parotid gland. It is flattened and disklike. The infraorbital gland is located at the caudal orbit. The duct of both glands join to open into the conjunctiva at the lateral canthus of the eye (Bivin et al. 1979; Hebel & Stromberg 1986f; Komarek et al. 2000b; Sharp & LaRegina 1998).

Hearing

Rats can hear sounds of high frequency (60–80 kHz) and use ultrasound frequencies for social vocalizations. They have a high pitched squeak with two types of call: one above 20 kHz (the limit of human hearing) and one at 50 kHz. Both males and females use the 50 kHz sound during copulatory behavior. Ultrasonic vocalizations (80 kHz) are used for maternal–young interactions, sexual–territorial interactions or as a warning signal. Rats can produce this noise by a whistling associated with respiration (Koolhaas 1999).

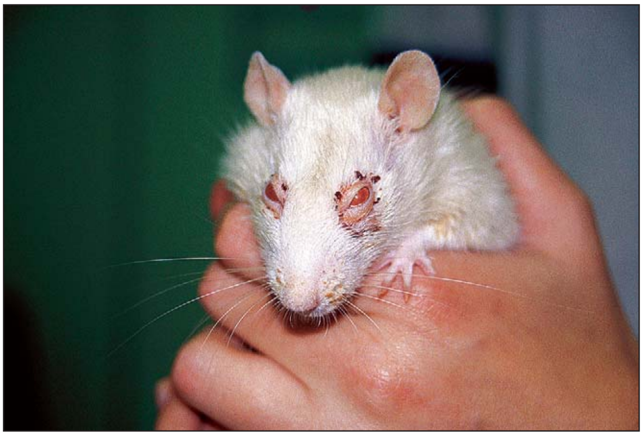


Figure 10.25 • Chromodacryorrhea in an aged rat. Stress or illness causes the Harderian gland to hypersecrete a porphyrin red pigment creating the impression of red tears.

Ears

The pinna is covered by thin, short hairs. The tympanic cavity is large, as in most rodents. A gland called the zymbal gland lies at the ear base (Hebel & Stromberg 1986f).

CLINICAL NOTE

As humans cannot hear high frequencies care should be taken with high pitched and ultrasound noises emitted from equipment like televisions, video recorders, and computers. Fire alarms have been found to affect estrous cycles in rats, so makes of lower frequencies have been designed for use in laboratories (Gamble 1976). Rats are less sensitive than humans to noises below 1000Hz so will be less affected by noises like air conditioning (Baker 1979).

Olfaction

The olfactory lobes of the brain are large and over 50% of the nasal cavity is lined by olfactory epithelium, giving rats their acute sense of smell. Rats, like all rodents, use their scent glands, feces, urine, and vaginal secretions for olfactory communication.

CLINICAL NOTE

Rats, like all rodents, are obligate nose breathers and rely on healthy nares not only for respiration but also for olfaction and feeding. Hence, the rapid debilitating effects of respiratory disease (Harkema & Morgan 1996).

Touch

The vibrissae are extremely sensitive to touch and are as sensitive as the fingertips of primates. These, combined with the acute sense of smell, compensate for the lack of vision. They are used continually in order to gauge distance and in locomotion (Koolhaas 1999).

INTEGUMENT

The hair is divided into guard hairs and undercoat. The wild color is agouti, meaning brown and black on top with a lighter underbelly. The rat has tactile vibrissae which are essential for the animal's orientation. They have sensory bulbs at their base, and an extensive nerve and blood supply. There are 50 to 60 of them located on each side of the upper lip and nose in 8 to 10 rows and they are innervated by the infraorbital nerve. Smaller tactile hairs are also found on the lower lip, chin, and upper eyelid (Hebel & Stromberg 1986e).

The epidermis is thin and mostly covered with hairs. The dorsal skin has a higher water content but less lipid than the abdominal skin. Numerous mast cells are found throughout the dermis and subcutis (except the tail). The subcutis should only contain moderate amounts of white fat. Brown fat is deposited between the scapulae, ventral neck and axillae in the thoracic inlet and inguinal region (Hebel & Stromberg 1986e; Komarek et al 2000b).

Skin glands

The sebaceous glands are found around the hair follicles. Modified sebaceous glands are found in the region of the oral commissure, the anus and prepuce, and around the teats. Auditory sebaceous glands, called Zymbal's glands open into the external ear canal (Hebel & Stromberg 1986e).

Sweat glands are only found around the footpad where they help in creating friction. The epithelium of these glands has only one cell type and so are unique among comparable species (Hebel & Stromberg 1986e). Rats have no specialized scent glands but produce pheromones through urine, feces, milk, and skin. These affect reproductive behavior, dominance, and territorial behavior.

Zymbal's gland

These are large modified sebaceous glands that surround the base of the ear. Tumors of this gland can occur as an ulcerated mass within the external ear canal and these may become so large as to involve the whole face and neck (Altman & Goodman 1979).

CLINICAL NOTE

Older entire male rats often develop yellow-brown sebaceous secretions along the dorsum, which are often confused with mites or lice. This effect is enhanced by testosterone and inhibited by estrogen (Fallon 1996).

KEY POINTS

- Open rooted, yellow incisors; closed rooted molars
- Lower incisors are 2 to 3 times longer than upper
- Stomach has glandular and non-glandular portions
- No gall bladder
- Female has a duplex uterus and urethral orifice is separate from vulva
- Extensive mammary tissue from axilla to groin in female
- Acute sense of smell and hearing
- Prominent Harderian gland which hypersecretes "red tears"

REFERENCES

Altman, N. H., & Goodman, D. G. (1979) Neoplastic diseases. In H. J. Baker, J. R. Lindsey & S.H. Weisbroth (eds.), *The laboratory rat*. Vol. 1, Biology & diseases. New York: Academic Press. pp. 334–376.

Baker, D. E. (1979) Reproduction and breeding. In H. J. Baker, J. R. Lindsey & S.H. Weisbroth (eds.), *The laboratory rat*. Vol. 1, Biology & diseases. New York: Academic Press. pp. 154–167.

Bivin, W. S., Crawford, M. P., & Brewer, N. R. (1979) Morphophysiology. In H. J. Baker, J. R. Lindsey, & S. H. Weisbroth (eds.), *The laboratory rat*. Vol. 1, Biology & diseases. New York: Academic Press. pp. 74–100.

Cheeke, P. R., & Amber, J. W. (1973) Comparative calcium excretion by rats and rabbits. *Journal of Animal Science 37*, 450–454.

Del Campo, C. H., & Ginther, O. J. (1972) Vascular anatomy of the uterus and ovaries and the unilateral luteolytic effect of the uterus: Guinea pigs, rats, hamsters and rabbits. *American Journal of Veterinary Research* 33, 2561–2578.

Fallon, M. T. (1996) Rats and mice. In K. Laber-Laird, M. M. Swindle & P. Flecknell (eds.), *Handbook of rodent and rabbit medicine*. Oxford: Pergamon. pp. 1–39.

Gamble, M. R. (1976) Fire alarms and oestrous in rats. *Laboratory Animals 10*, 161–163.

Greene, E. C. (1962) Gross anatomy. In E.J. Farris & J.Q. Griffith (eds.), *The rat in laboratory investigation*, 2nd edn. New York: Hafner. pp. 24–50.

Harkema, J. R., & Morgan, K. T. (1996) Normal morphology of the nasal passages in laboratory rodents. In T. C. Jones, D. L. Dungworth & U. Mohr (eds.), *Monographs on pathology of laboratory animals*, 2nd edn. Berlin: Springer-Verlag. pp. 3–18.

Harkness, J.E., & Wagner, J.E. (1995) *The biology and medicine of rabbits and rodents*, 4th edn. Baltimore: William & Wilkins. Biology and husbandry – the rat; pp. 65–73.

Hebel, R., & Stromberg, M. W. (1986a) *Anatomy and embryology of the laboratory rat*. Worthsee, Germany: Biomed Verlag. Osteology A; pp. 1–22.

Hebel, R., & Stromberg, M. W. (1986b) *Anatomy and embryology of the laboratory rat*. Worthsee, Germany: Biomed Verlag. B Myology; pp. 25–45.

Hebel, R., & Stromberg, M. W. (1986c) *Anatomy and embryology of the laboratory rat*. Worthsee, Germany: Biomed Verlag. C Digestive system; pp. 46–55.

Hebel, R., & Stromberg, M. W. (1986d) *Anatomy and embryology of the laboratory rat*. Worthsee, Germany: Biomed Verlag. D Respiratory system; pp. 58–64.

Hebel, R., & Stromberg, M. W. (1986e) *Anatomy and embryology of the laboratory rat*. Worthsee, Germany: Biomed Verlag. M The integument; pp. 225–229.

Hebel, R., & Stromberg, M. W. (1986f) *Anatomy and embryology of the laboratory rat*. Worthsee, Germany: Biomed Verlag. L Sensory Organs; pp. 218–223.

Hebel, R., & Stromberg, M. W. (1986g) *Anatomy and embryology of the laboratory rat*. Worthsee, Germany: Biomed Verlag. E, F, G Urinary, male and female reproductive organs; pp. 65–87.

King, G. M., & Custance, D. R. (1982) *Colour atlas of vertebrate anatomy*. Oxford: Blackwell Scientific. The rat; pp. 6.1–6.18.

Komarek, V. (2000) Gross anatomy. In G. J. Krinke (ed.), *The laboratory rat*. San Diego, Calif.: Academic Press. pp. 253–277.

Komarek ,V., Gembardt, C., Krinke, A., Mahrous, T.A., & Schalti, P. (2000b) Synopsis of the organ anatomy. In G. J. Krinke (ed.), *The laboratory rat*. San Diego, Calif.: Academic Press. pp. 283–323.

Koolhaas, J. M. (1999) The laboratory rat. In T. Poole (ed.), *The UFAW handbook on the care and management of laboratory animals*, 7th edn. Vol. 1. pp. 313–331.

Maeda, K., Ohkura, S., & Tsukamura, H. (2000) Physiology of reproduction. In G. J. Krinke (ed.), *The laboratory rat*. San Diego, Calif.: Academic Press. pp. 145–171.

Percy, D. H., & Barthold, S. W. (2001) *Pathology of laboratory rodents and rabbits*, 2nd edn. Ames: Iowa State University Press. Rat; pp. 107–158.

Popesko, P., Rajtova, V., & Horak, J. (1992) *A colour atlas of anatomy of small laboratory animals*. Vol. 2. Aylesbury, UK : Wolfe. Rat, mouse, hamster; pp. 11–105.

Schour, I., & Massler, M. (1962) The teeth. In Farris & Griffith (eds.), *The rat in laboratory investigation*, 2nd edn. New York: Hafner. pp. 104–160.

Sharp, P. E., & LaRegina, M. C. (1998) Important biological features. In M. A. Suckow (ed.), *The laboratory rat*. Boca Raton, Fla.: CRC Press. pp. 1–19.

Yu, B. P. (1994) How diet affects the ageing process. *Proceedings of the Society for Experimental Biology and Medicine 205*, pp. 97–105.

11

Hamsters

INTRODUCTION

In comparison to the rat and guinea pig, the Syrian hamster (*Mesocricetus auratus*) has only recently been domesticated (Derrell Clark 1987). The first wild Syrian hamsters were collected only 75 years ago from the north-west Syrian desert. Our current pet and laboratory hamsters have since been bred from a limited gene pool of 3 littermates captured in 1930, 11 more captured in 1971 and 3 more in 1978 (Derrell Clark 1987; Fulton 1968; Nowak 1999). The original ones were a reddish brown color and hence were originally called Golden hamsters. The development of a vast variety of different colors since then means that they are now more correctly called the *Syrian hamster.*

The Syrian hamster is unique among pet rodents in that they are not gregarious and best kept singly because the female will attack the male except when in estrus. They are also nocturnal. As they can be quite aggressive when disturbed from sleep they have earned an unfair reputation for being pugnacious (Lipman & Foltz 1996).

Hamsters and gerbils are from the family Cricetidae and differ from rats and mice in having a haired tail and molar teeth with cusps arranged in two parallel rows instead of three (Derrell Clark 1987).

THERMOREGULATION

The recommended temperature range for the hamster is 20–24° C, with a relative humidity of 54–55%. As they are nocturnal, the best photoperiod for optimal reproduction used in laboratories is 14 hours night and 10 hours day. This is in contrast to other rodents, which do better with 12 hour periods. Photoperiod appears to be mediated through the pineal gland. Despite their dozy appearance by day hamsters are extremely active at night. In fact, fit hamsters have been known to travel several kilometers on an exercise wheel.

Hamsters have a patch of brown fat over the scapula blades that extends from the cervical to the mid-thoracic region. In the abdominal region the adrenal glands, renal hila, and parts of the ureters are also sheathed in brown fat. During periods of cold the rich blood supply to this tissue increases and the weight of the tissue increases (Hoffman 1968). Tissue protein levels increase while fat levels decrease. The reverse happens in warm weather (Bivin et al. 1987).

Hibernation

If environmental temperatures are lower than 5° C hamsters can enter a temporary hibernation, thus lowering their body temperature, heart, and respiratory rate. They can, however, remain sensitive to touch during this period (Lipman & Foltz 1996). This pseudo-hibernation can also be stimulated by shorter day length and less light. The converse can also be true in that, exposed to warm ambient temperature, the hamster will go into a deep sleep – and if aroused suddenly will be most pugnacious (Hoffman 1968).

GENERAL EXTERNAL ANATOMY

The Syrian hamster is short tailed and stocky, with a very large amount of loose skin dorsally. The body weight of the mature male is about 85–110 g; the female is bigger at 95–120 g (Derrell Clark 1987; Nowak 1999; Whittaker 1999). The original wild hamster was reddish-gold with a gray ventrum, but many color varieties now exist from cinnamon, cream, and piebald to albino (Harkness & Wagner 1995) (Fig. 11.1).

The eyes are black and exopthalmic and the incisor teeth are colored yellow due to iron pigments (Derrell Clark 1987).

External genitalia

The sexually mature male has an enlarged, rounded posterior end when the testes are descended, pigmented flank glands, and a longer anogenital distance than the female. The female has a more pointed posterior, less prominent flank glands, and a completely separate vaginal and urethral opening (Bivin et al. 1987; Lipman & Foltz 1996) (Fig. 11.2).

Figure 11.1 • Many color varieties of hamster now exist, hence the name change from Golden to Syrian hamster.

SKELETAL SYSTEM

The vertebral formula is 7 cervical, 13 thoracic, 6 lumbar, 4 sacral and 13–14 caudal (Bivin et al. 1987). There are four digits in the front feet and five in the back feet. There are seven sternal and six post-sternal ribs (Figs. 11.3 and 11.7). Two sternopericardial ligaments connect the pericardial sac to the sternum.

Abdominal cavity

This is the largest body cavity, extending from the diaphragm to the pelvic cavity. The greater omentum is thin and fatty and extends from the greater curvature to the duodenum and transverse colon.

CARDIOVASCULAR SYSTEM

The heart is in the midline and is in contact with the thoracic wall at ribs 3–5 (Bivin et al. 1987). The heart rate can vary from 250 to 500 beats per minute. There are three main branches arising from the aortic arch (innominate, left common carotid, and left subclavian), and three caval veins (two cranial vena cavae and one caudal vena cava) enter the right atrium. As in the rat, the pulmonary veins contain sheaths of cardiac muscle fibers within the vessel walls (Bivin et al. 1987; Magalhaes 1968).

Venepuncture

The blood volume of the Syrian hamster is about 78 ml/kg (Bivin et al. 1987). Due to lack of a tail, vein blood sampling can be difficult, but the saphenous or jugular veins can be tried (McClure 1999). Laboratory animals are often bled via the orbital venous sinus and cardiac puncture, but this is not recommended in pet animals (Whittaker 1999). Hamsters have a rapid coagulation time so heparin may need to be used.

RESPIRATORY SYSTEM

The respiratory rate is approximately 30–32 breaths per minute. Hamsters have well-developed nasal turbinates that are lined by nasal mucosa whose function is to filter and humidify the incoming air and also to warm or cool the air before it passes to the lungs. This is aided by many nasal glands which open into the external nares. Like the rat, they also have well-developed olfactory epithelium and bulbs, giving the hamster its keen sense of smell (Bivin et al. 1987; Magalhaes 1968). The lungs have a large single left lobe

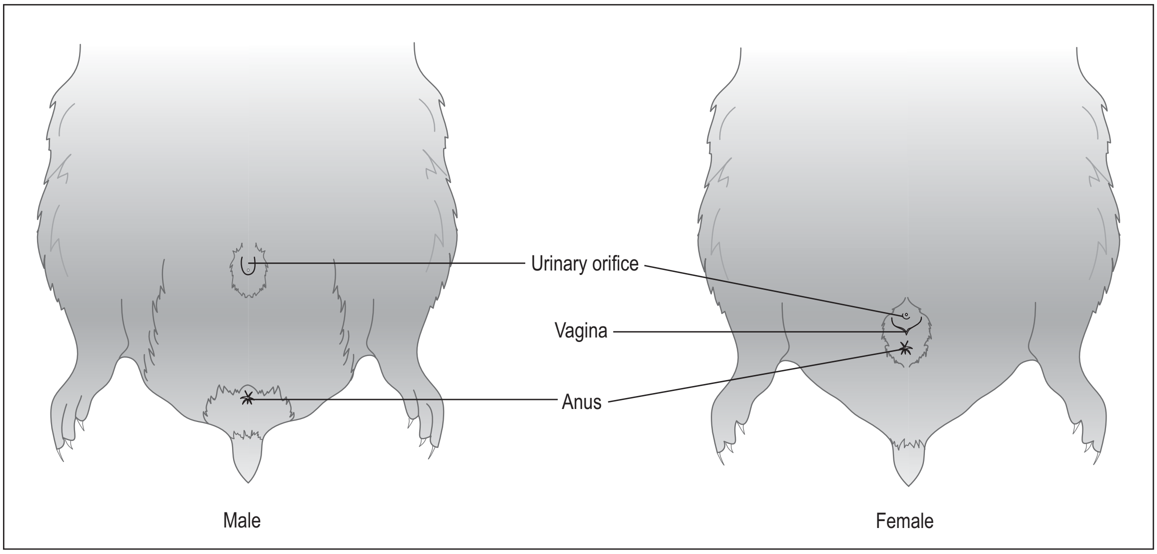


Figure 11.2 • External genitalia. (a) The male has a longer anogenital distance, (b) The female has a short anogenital distance with a completely separate vaginal and urethral opening.

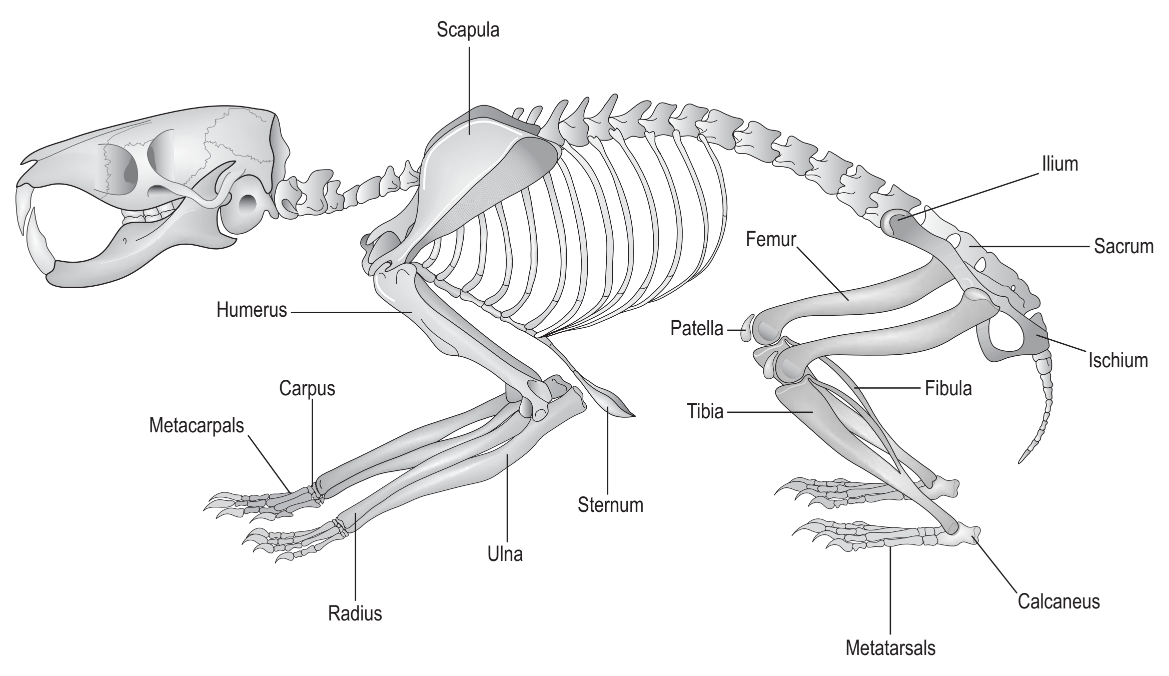


Figure 11.3 • Skeleton of the Syrian hamster (*Mesocricetus auratus*). From Popesko, P., Rajtova, V., & Horak, J. (1990) A colour atlas of anatomy of small laboratory animals. Vol. 2. Aylesbury, UK: Wolfe with permission.

with four lobes on the right: the cranial, middle, caudal, and accessory (Bivin et al. 1987). The thymus lies in the cranial mediastinum and consists of two lobes that decrease in size with age (Fig. 11.9).

DIGESTIVE SYSTEM

Feeding patterns

Hamsters are omnivorous and coprophagic (Lipman & Foltz 1996). They feed in 5-minute bursts followed by a 2-hour fast (Bivin et al. 1987). Food intake is about 5–7 g daily and water intake is about 10 ml. The hamster has evolved certain patterns of behavior consistent with a burrowing and hoarding desert animal. Unlike the greedy rat, they do not increase their food intake following periods of fasting; however, they do hoard away more food in case of further deprivation later (Newcomer et al. 1987).

Dentition

The oral aperture can stretch from 12 mm vertically to 17 mm horizontally. The dental formula is 1/1,0/0,0/0,3/3 (Bivin et al. 1987; Lipman & Foltz 1996). The hamster has open-rooted yellow incisors and rooted (brachiodont) molars. The shorter upper incisors can be replaced in 1 week whereas the longer lower incisors take 2.5–3 weeks to regrow. The diastema is longer in the maxilla than the mandible (Figs. 11.4 and 11.5). The mandibular symphysis is freely movable and may not fuse (Harkness & Wagner 1995).

Hamsters (Cricetidae) differ from rats and mice (Muridae) in having molar cusps in two parallel longitudinal rows instead of being arranged in three rows (Derrell Clark 1987). The crowns allow retention of food, which makes hamsters, like humans, susceptible to caries. Male hamsters are more prone to caries than females (Bivin et al. 1987).

The tongue is well developed and very flexible. The muscular bulge at the base contains the small hyoid bone. There are four types of lingual papillae: filiform, fungiform, foliate, and vallate. The major salivary glands are submaxillary, parotid, and sublingual (Bivin et al. 1987; Magalhaes 1968).

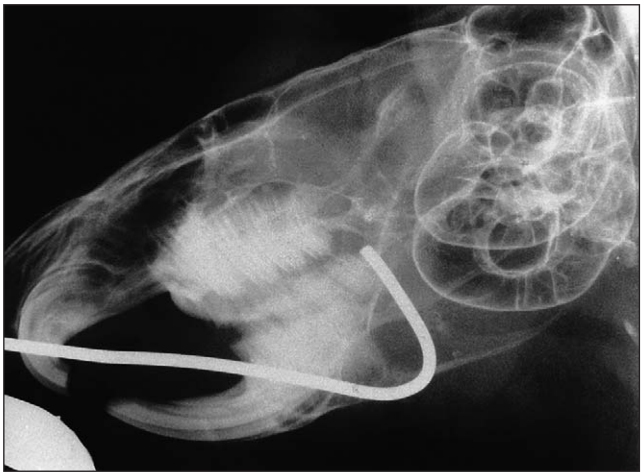


Figure 11.4 • Radiograph of hamster that got the wire of it's water bottle trapped in the pouch. Note the large tympanic bulla typical of a nocturnal species.

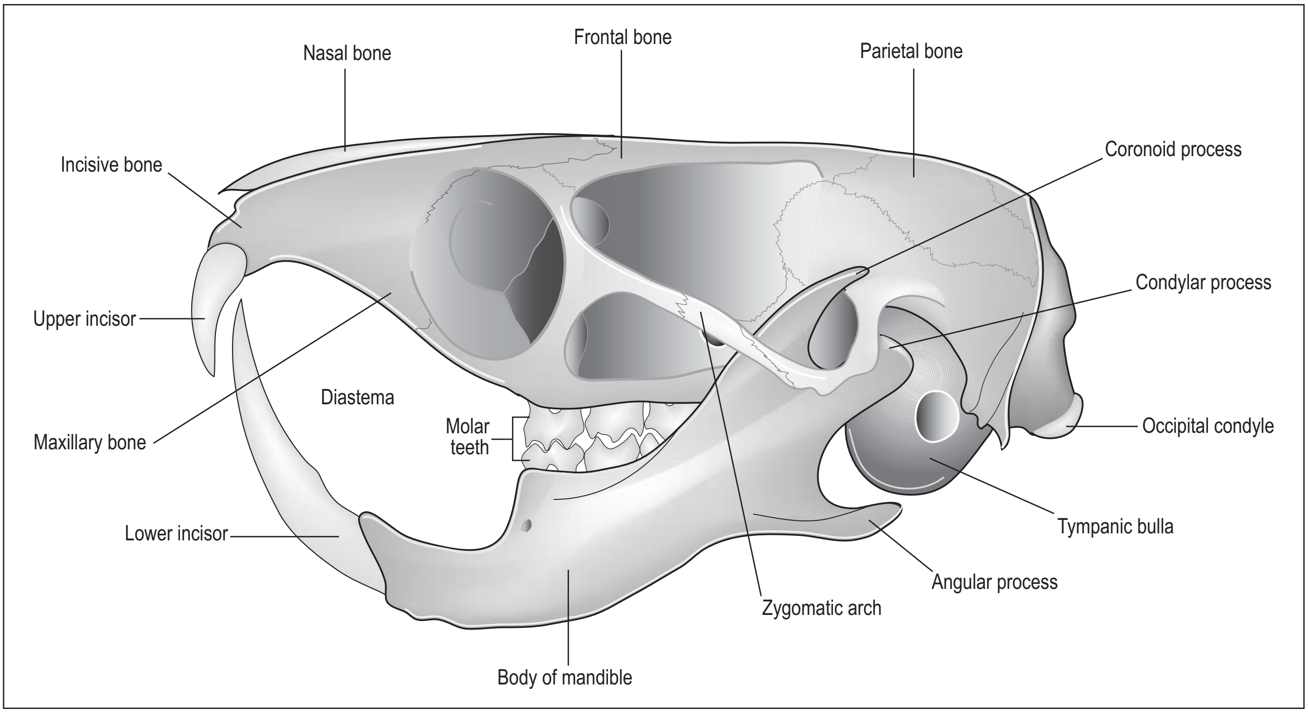

Nasal bone
Frontal bone
Parietal bone
Incisive bone
Coronoid process
Upper incisor
Condylar process
Diastema
Maxillary bone
Molar teeth
Occipital condyle
Lower incisor
Tympanic bulla
Angular process
Zygomatic arch
Body of mandible

Figure 11.5 • Skull of Syrian hamster (*Mesocricetus auratus*). From Popesko, P., Rajtova, V., & Horak, J. (1990) A colour atlas of anatomy of small laboratory animals. Vol. 2. Aylesbury, UK: Wolfe with permission.

Cheek pouch

The Arabic term for the hamster in its native Syria is "*master of the saddle bags*" on account of their using their pouches to transport food, bedding, and even young in times of danger (Harkness & Wagner 1995; Lipman & Foltz 1996; Nowak 1999). The pouches are highly distensible invaginations of the lateral buccal epithelium, which extend from the mouth as far as the dorsocaudal scapulae (Harkness & Wagner 1995) (Fig. 11.6).

The pouch measures 4–8 mm wide when empty and 20 mm when full (Bivin et al. 1987). When filled, the pouches cover the parotid gland, masseter muscles, and lateral neck and shoulder muscles. The mucosa has pale pink folds and is extremely vascular, being supplied by three branches of the external carotid artery. It has, however, no lymphatic supply or adjacent lymph nodes. It is transparent with no hair or glands (Magalhaes 1968).

Cheek pouches are used in research as they are immunologically privileged sites. This is thought to be due to the poor lymphatic blood supply and the lack of glandular tissue. The fact that it can also be easily everted makes it very useful for research on microcirculation, tumors, and transplant surgery (Harkness & Wagner 1995).

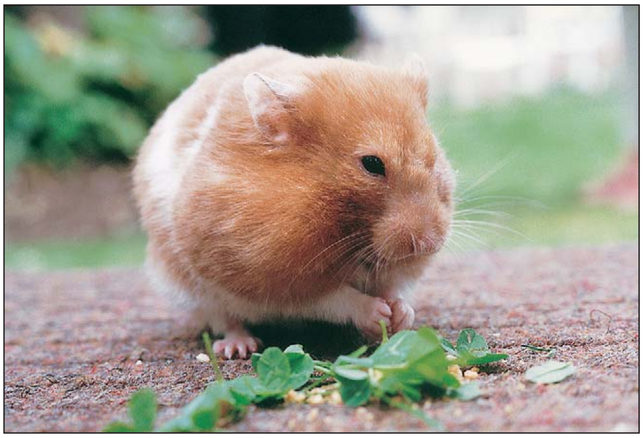


Figure 11.6 • Syrian hamster with bulging cheek pouch.

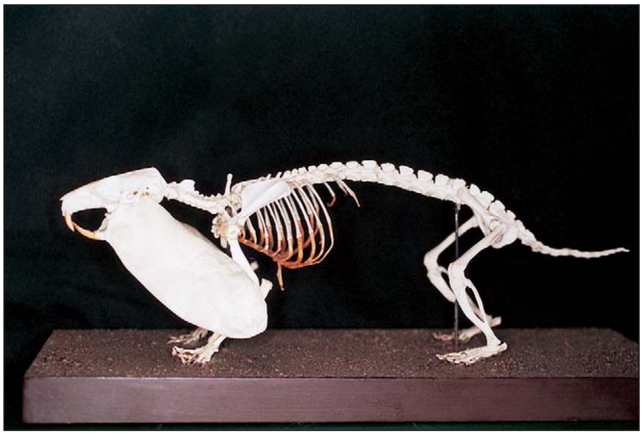


Figure 11.7 • Skeleton of European hamster (*Cricetus cricetus*) with cast made to show the extent of the cheek pouches. The European hamster is three to four times larger than the Syrian hamster. Its cheek pouches measure about 60 mm × 15 mm and have a carrying capacity of 20–30 g!

The wall is composed of four layers: keratinized, stratified squamous epithelium, dense collagenous connective tissue, striated muscle fibers, and loose areolar connective tissue where it joins the underlying structures. There are blood vessels and nerves in the connective tissue and muscle. The pouch is emptied by the massaging action of the front feet along with the tongue (Bivin et al. 1987; Magalhaes 1968).

Stomach

The esophagus is lined by keratinized squamous epithelium and leads into the non-glandular part of the stomach. The stomach has two compartments: the non-glandular and the glandular. They are distinguished by a muscular-like sphincter, which may regulate passage of ingesta between the two sections. The esophageal opening lies just cranial to this constriction. The lesser curvature of the stomach is almost non existent as the cardia is located quite near to the pylorus, making vomiting impossible (Hoover et al. 1969; Lipman & Foltz 1996). The total dimensions of the stomach are approximately 3.5×2 cm (Hoover et al. 1969).

Forestomach (non-glandular)

The forestomach is lined by squamous epithelium and a thick muscular layer that is similar to the rumen, although it lacks ruminal papillae. The bacteria are mainly gram-positive, with some gram-negative coliforms (Bivin et al. 1987). The pH is higher than in the glandular stomach, which indicates that mixing of food from both areas does not occur (Hoover et al. 1969).

The presence of volatile fatty acids (mainly acetic) in the forestomach indicates that some fermentation does go on here, with some being absorbed. However, this fermentation role may not be very large as food only stays in the forestomach for about 1 hour (Hoover et al. 1969).

Glandular stomach

This resembles the stomach in the normal monogastric animal and is lined by glandular mucous membranes.

Intestines (Figs. 11.8 and 11.9)

The jejunum is 2.5 times longer than the duodenum (Bivin et al. 1987). The ileum is short and leads into the cecum, which is sacculated and divided into an apical and basal portion. The cecum bends back on itself and divides into four valves (Bivin et al. 1987). The normal bacterial flora are *Bacteroides* spp. and lactobacillus, plus a few coliforms and clostridia. The pH here is higher than in the non-glandular stomach, which suggests either more active fermentation or perhaps better buffering.

Liver and pancreas

The liver has four lobes: right and left medial, and right and left lateral. The gall bladder is located in the ventral median lobe in the right cranioventral section. The pancreas is well defined but often yellow-white in color, owing to associated adipose tissue.

URINARY SYSTEM

Hamsters are adapted for the desert environment by having both renal and respiratory conservation mechanisms, but unlike some desert rodents they cannot survive on metabolic water alone (Newcomer et al. 1987).

The kidneys are reddish brown and bean shaped. The right kidney lies at the level of L2–L4 and the left kidney lies at L3–4. The kidney is unipapillate, having a very long papilla extending out into the ureter (Bivin et al. 1987; Magalhaes 1968). This is an adaptation to an arid environment as it produces very concentrated urine and prevents dehydration.

Urine is thick and creamy with a normal pH of 5.1–8.4. Hamsters usually produce up to 7 ml of urine per day but this can increase up to 75 ml/day in hamsters with diabetes (Harkness & Wagner 1995). Proteinuria can be found even in normal hamsters.

REPRODUCTIVE SYSTEM

Hamsters can reach sexual maturity from 6 weeks of age but for optimal breeding it is best if the male is 10–12 weeks and the female at least 8–10 weeks before being bred. Breeding ceases after 14 months of age.

Male

The anogenital distance is longer in the male, which has a more prominent genital papilla. There is a baculum or os penis consisting of two lateral prongs and a dorsal prong.

In mature males a thick fat pad covers the proximal end of the testicle and almost half the epididymis (the dorsomedial side of the testicle), giving the hamster a very large scrotal silhouette (Bivin et al. 1987; Ferm 1987). Male accessory glands include the ampulla glands, seminal vesicles, coagulating glands, three lobed prostate, and bulbourethral glands. Like other rodents, the adult male hamster produces a urethral plug (Kent 1968).

CLINICAL NOTE

Hamsters exposed to natural daylight and temperature will show seasonal variation in testicle size, having the lowest masses in winter. Hence, the number of anxious pet owners presenting at veterinary clinics in summer concerned that their “female” hamster has suddenly developed two enormous tumors!

Female

The urinary opening is cranial and the anus is caudal, with the vaginal opening in between. The vagina has a pair of vaginal pouches that extend caudally, terminating at the level of

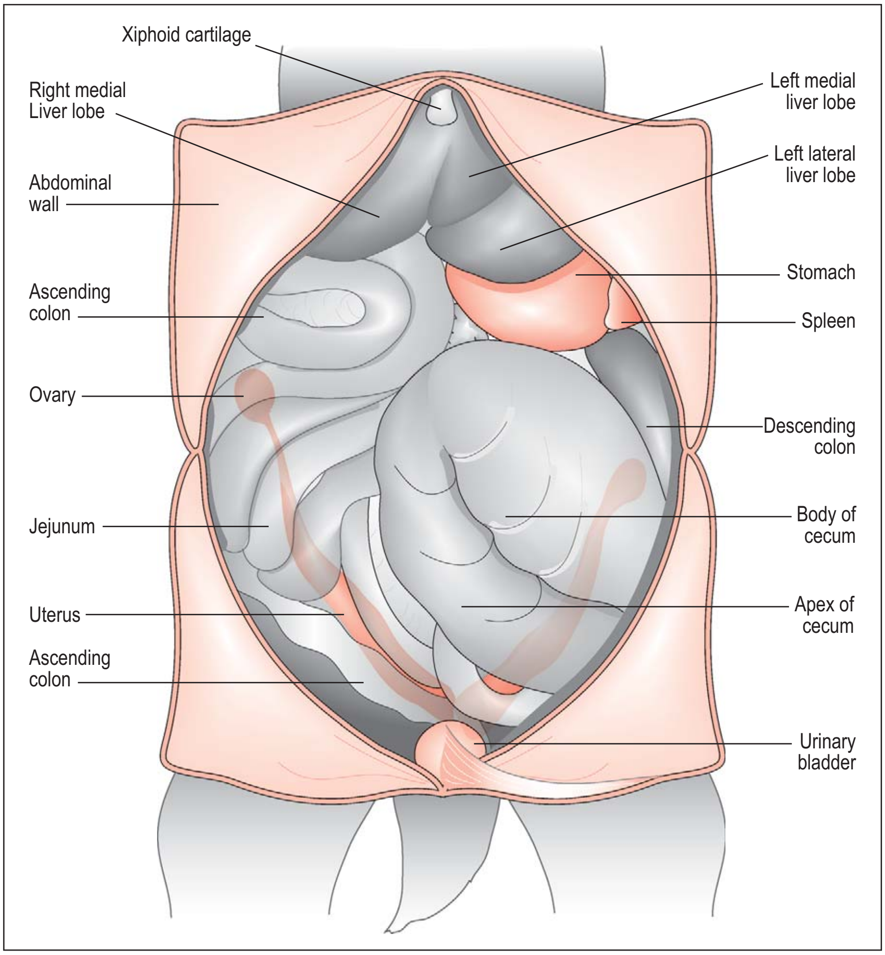


Figure 11.8 • Ventral view of female hamster showing abdominal viscera. The right uterine horn is shown, *shaded*, behind the intestines. From Popesko, P., Rajtova, V., & Horak, J. (1990) A colour atlas of anatomy of small laboratory animals. Vol. 2. Aylesbury, UK: Wolfe with permission.

the vaginal orifice. Like the rat, the uterus is duplex and leads into two cervices with the undivided part being 7–8 mm long (Bivin et al. 1987; Ferm 1987; Kent 1968). There are 6 or 7 pairs of mammary glands extending from the thorax to the inguinal region (Fig. 11.10). Flank glands are present but are less prominent than in the male, owing to their lighter pigmentation.

The ovaries are oval, situated dorsolateral to the kidneys, and are completely enclosed in a fat-filled ovarian bursa. The oviduct is long and tightly coiled. Like in the guinea pig and rat, the uterine artery in the hamster provides a major portion of the blood supply to the ovary (Bivin et al. 1987). In some hamsters, coils of the ovarian and uterine arteries anastomose close to the ovary (Del Campo & Ginther 1972; Ferm 1987).

Estrous cycle

The hamster is seasonally polyestrous and has a very regular 4 day estrous cycle. Ovulation occurs about 12 hours after the luteinizing hormone (LH) surge, usually resulting in the release of the ova at night, which is in keeping with the hamster's nocturnal habits. The female hamster will become sexually receptive only for the few hours post ovulation. On the 2nd day of estrus she will produce a white stringy discharge which becomes waxier on day 3. At the end of estrus the female produces a copious white, viscous discharge that has a distinct odor (Harkness & Wagner 1995; Kent 1968).

The usually pugnacious female will tolerate the male at peak estrus and copulation takes place immediately after introduction of the male. This usually last 30 minutes and a copulatory plug can be observed after mating. Pseudopregnancy can occur after infertile mating.

CLINICAL NOTE

Although the vagina and cervix do show cyclical changes in response to ovarian hormones, vaginal cytology is complicated by the presence of vaginal pouches. These paired vaginal pouches collect exfoliative cells and leukocytes, so only smears made daily would be accurate (Whittaker 1999).

Gestation

The Syrian hamster has the shortest known gestation for any eutherian mammal, being only 15–18 days (Lipman & Foltz 1996; Newcomer et al. 1987; Whittaker 1999). The young are born altricial, with closed eyes and earflaps, but

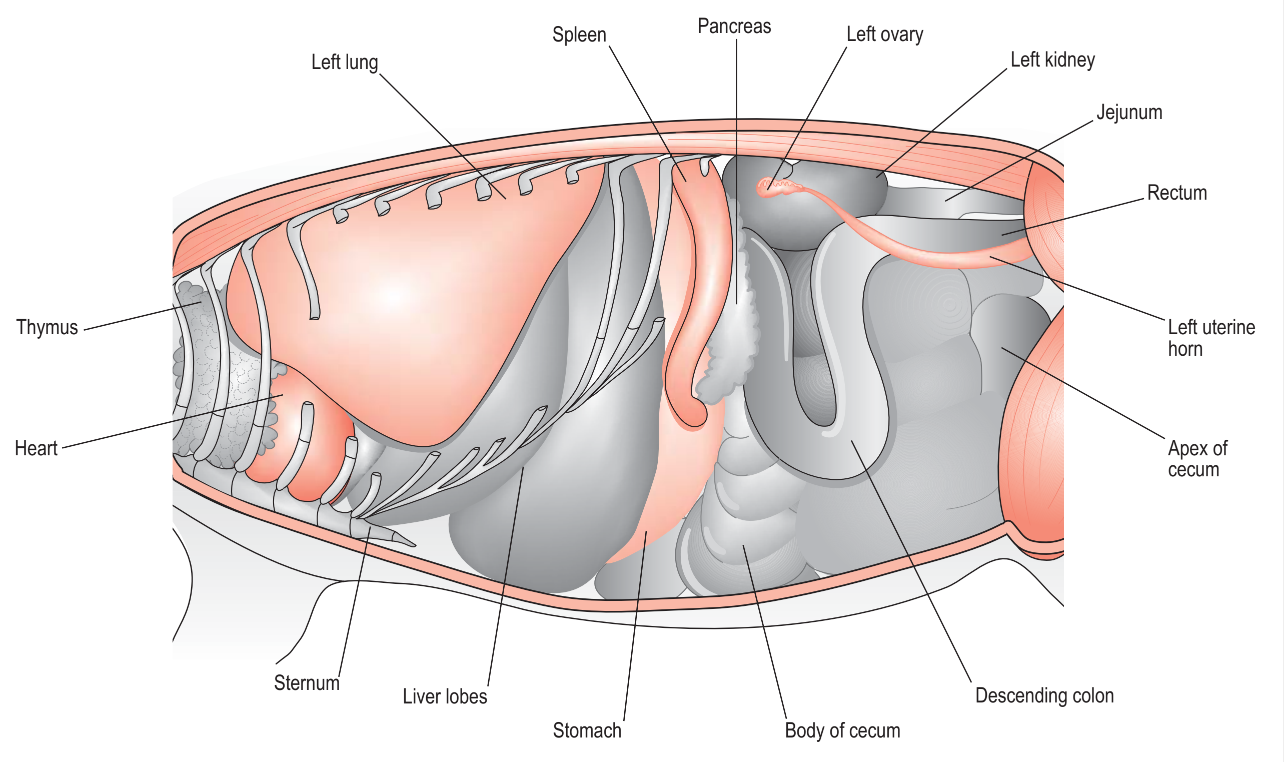

Left lung
Spleen
Pancreas
Left ovary
Left kidney
Jejunum
Rectum
Thymus
Left uterine horn
Heart
Apex of cecum
Sternum
Liver lobes
Stomach
Body of cecum
Descending colon

Figure 11.9 • Lateral left side of abdominal cavity of female hamster (ribs removed). From Popesko, P., Rajtova, V., & Horak, J. (1990) A colour atlas of anatomy of small laboratory animals. Vol. 2. Aylesbury, UK: Wolfe.

do have sharp teeth (Fig. 11.11). Pups weigh 2–3 g at birth and their eyes and ears open at 5 and 15 days, respectively. Weaning is at around 3 weeks (Harkness & Wagner 1995; Kent 1968).

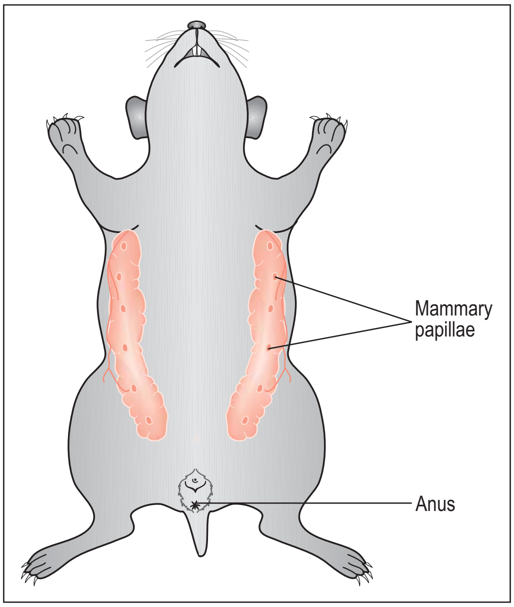

Mammary papillae
Anus

Figure 11.10 • Ventral view of mammary glands in the female hamster. From Popesko, P., Rajtova, V., & Horak, J. (1990) A colour atlas of anatomy of small laboratory animals. Vol. 2. Aylesbury, UK: Wolfe with permission.

ENDOCRINE SYSTEM

The thryoid gland is bilobed and located at the level of the first tracheal cartilage. There are two parathyroid glands in its lateral margins. The adrenal glands lie craniomedial to the kidney and are embedded in adipose tissue. Unlike in most rodents, these glands are bigger in the male than the female (Bivin et al. 1987). There is a higher incidence of adrenocortical hyperplasia and adenomas in the Syrian hamsters

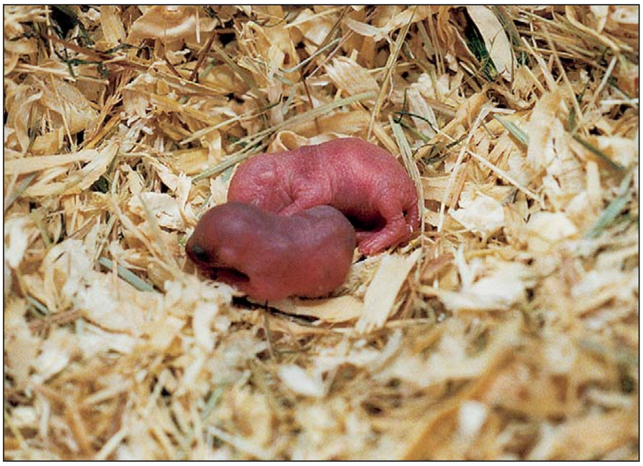


Figure 11.11 • Hamster young are born altricial – both their eyes and earflaps are closed.

than any other rodent and these occur more commonly in elderly (2- to 3-year-old) male hamsters.

SENSES

Sight

Being nocturnal, vision is less important than hearing, olfaction, and sensation. The hamster has a panoramic visual field. A large orbital venous sinus is present and this is used for blood sampling in laboratory animals (Bivin et al. 1987).

Hearing and touch

In common with all rodents, hamsters have large tympanic bullae giving them a keen sense of hearing (Fig. 11.4). Sensitive vibrissae are the main channel for somatic sensory input.

Taste

Hamsters dislike saline solutions but love sugary foods (Carpenter 1956). They will also show preference for ethanol, which unlike most other rodents they can metabolize well on account of their having two to three times more alcohol dehydrogenase in their liver than do rats. It is thought that this may have evolved due to the storage of fermentative grains hoarded underground in their burrow. This high tolerance to alcohol means that scientists have been unable to use the hamster as a model for alcohol-induced diseases (Newcomer et al. 1987).

Olfaction

Being nocturnal, hamsters have a keen sense of smell and this is enabled by the extensive olfactory epithelium in the caudal nasal cavity and the vomeronasal (Jacobson's) organ.

Jacobson's organ is a 7 mm long tubular structure that is located bilaterally in the rostroventral nasal septum and completely enclosed in a bony capsule. The cranial end communicates with the nasal cavity rostrally. The medial wall of the lumen is lined by sensory olfactory epithelium with the vomeronasal nerve lying just beneath. Caudally, it connects with olfactory receptors lying in the ethmoturbinates (Bivin et al. 1987). This organ may play a role in pheromone behavior as well as olfaction as removal of the main and accessory olfactory bulbs completely removes sexual behavior (Bivin et al. 1987).

INTEGUMENT

The fur is soft and smooth, and the ears are bald and gray. Around the neck region the skin is very loosely attached and capable of extensive stretching.

The young are born altricial and hair growth starts at 9 days. There is soft underfur and this is covered by longer and thicker guard hairs. The hair is sparse on the feet and tail and there are fine hairs on the pinnae. The flank glands have short sparse hairs, which are often darkly covered, more so in the male. Cranial sensitive vibrissae are essential for orientation, particularly in nocturnal mammals (Bivin et al. 1987).

Flank glands

These costovertebral glands consist of sebaceous glands, terminal hair, and pigment cells. They reach maximum size by 21 days in the female and 70 days in the male (Harkness & Wagner 1995). They are small and unpigmented in the young, becoming more developed and darkly pigmented in mature males (Fig. 11.12). Secretion of these glands is androgen dependent and the glands may play a role in lipogenesis, hair, and flank gland growth. They are much more prominent in the male and become damp when the male is sexually excited (Bivin et al. 1987; Lipman & Foltz 1996; Magalhaes 1968).

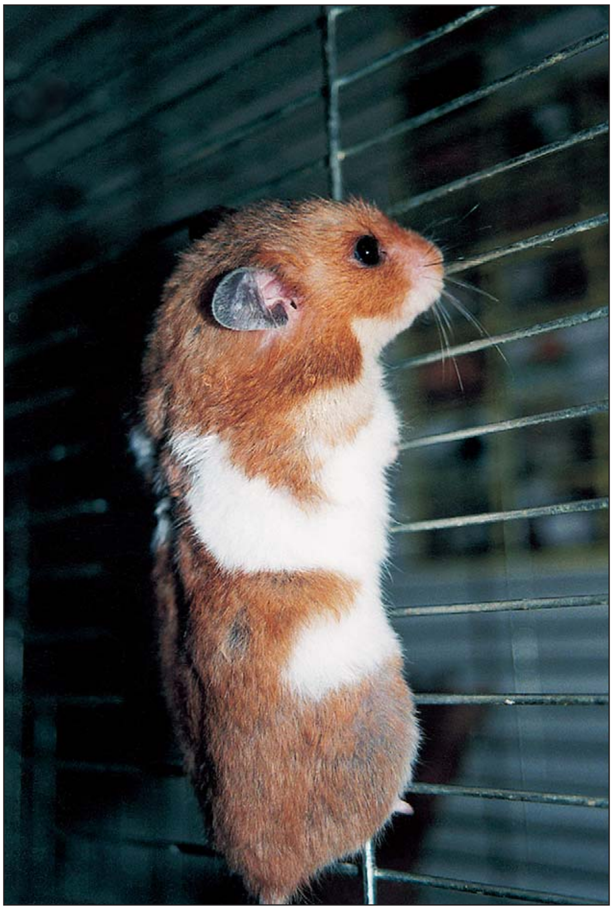


Figure 11.12 • Male Syrian hamster showing hip gland on lateral flank. They are more prominent and darkly pigmented in adult males.

KEY POINTS

- Open rooted incisors, closed molars
- Prominent hip glands
- Stomach divided into glandular and non-glandular portions
- Uterus is duplex, vaginal glands present
- Cheek pouches can extend as far caudal as shoulder blades
- Copious white discharge at end of estrous is normal in female

CHINESE HAMSTER

The Chinese hamster (*Cricetulus griseus*) was first used as a laboratory animal in China in 1919 in an attempt to identify types of pneumococci in human patients at the Peking medical college. A breeding stock of 10 males and 10 females was shipped to the USA in 1948, just before the establishment of the People's Republic of China (Chang et al. 1987). The discovery of hereditary diabetes in the Chinese hamster made them popular over the next two decades in diabetic research (Harkness & Wagner 1995). They are also the favored species for genetic research, having only 22 chromosomes (Lipman & Foltz 1996; Whittaker 1999).

The Chinese hamster is also known as the striped or gray hamster. They are small, weigh 30–35 g, with the female being about 10% smaller than the male (Chang et al. 1987; Harkness & Wagner 1995). The fur is grayish black with a dorsal stripe. They are quite pugnacious (especially the females) and so must be kept singly (Lipman & Foltz 1996). Like the Syrian they are polyestrous but with a slightly longer gestation period of 21 days.

RUSSIAN HAMSTER

The Russian hamster (*Phodopus sungorus*) has footpads covered in fur, hence the common name "hairy footed hamster" (Fig. 11.13). Adult males are about 11 cm long and have a body weight of 40–50 g; the females are smaller, being 9 cm long and about 30 g (Cantrell & Padovan 1987). The dorsal fur is gray, with a dark brown stripe down the middle from the nape to the tail base; ventrally the fur is white. The female has four pairs of mammary glands. As well as the flank glands they have a ventral sebaceous gland that is larger in males than females (Cantrell & Padovan 1987; Harkness & Wagner 1995).

The pelage will change to a white coat when exposed to natural light cycles and colder temperatures, an ability that evolved in order to provide camouflage in the snow (Cantrell & Padovan 1987). Under the influence of the pineal gland, increased melatonin production inhibits prolactin and causes the new fur to grow unpigmented as winter white. These hamsters do not hibernate but, if the temperature drops to 19° C for a few days, there is a decrease in body weight and the hamster goes into torpor for 4–8 hours each day in order to conserve energy (Cantrell & Padovan 1987).

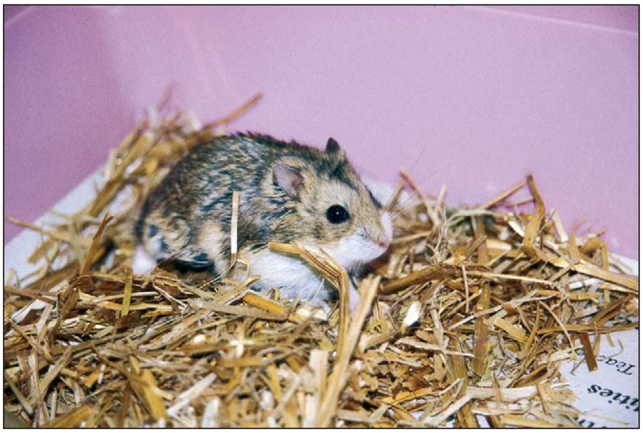


Figure 11.13 • Russian hamster (*Phodopus sungorus*).

This hamster is commonly used in laboratory research for studies in photoperiodism and the pineal gland. The male exhibits large testicles, enlarged accessory glands, and greater body weight when exposed to light for more than 13 hours per day (Cantrell & Padovan 1987).

REFERENCES

Bivin, W. S., Olsen, G. A., & Murray, K. A. (1987) Morphophysiology. In G. L. Van Hoosier & C. A. W. McPherson (eds.), *Laboratory hamsters*. Orlando, Fla.: Academic Press. pp. 9–42.

Cantrell, C.A., & Padovan, D. (1987) Other hamsters: Biology, care and use in research. In G. L. Van Hoosier & C. A. W. McPherson (eds.), *Laboratory hamsters*. Orlando, Fla.: Academic Press. pp. 369–373.

Carpenter, J. A. (1956) Species differences in taste preferences. *Journal of Comparative Physiology and Psychology 49*, 139–143.

Chang, A., Diani, A., & Conell, M. (1987) The striped or Chinese hamster: Biology and care. In G. L. Van Hoosier & C. A. W. McPherson (eds.), *Laboratory hamsters*. Orlando, Fla.: Academic Press. pp. 305–316.

Del Campo, C. H., & Ginther, O. J. (1972) Vascular anatomy of the uterus and ovaries and the unilateral luteolytic effect of the uterus: Guinea pigs, rats, hamsters and rabbits. *American Journal of Veterinary Research* 33, 2561–2578.

Derrell Clark, J. (1987) Historical perspectives and taxonomy. In G. L. Van Hoosier & C. A. W. McPherson (eds.), *Laboratory hamsters*. Orlando, Fla.: Academic Press. pp. 3–6.

Ferm, V. H. (1987) Genital system. In T. C. Jones, U. Mohair & R. D. Hunt (eds.), *Monographs on pathology of laboratory animals*. Berlin: Springer-Verlag. pp. 1–3.

Fulton, G. P. (1968) The golden hamster in biomedical research. In R. A. Hoffman, P. F. Robinson & H. Magalhaes (eds.), *The golden hamster – its biology and use medical research*. Ames: Iowa State University Press. pp. 3–15.

Harkness, J. E., & Wagner, J. E. (1995) *The biology and medicine of rabbits and rodents*, 4th edn. Baltimore: William & Wilkins. Biology and husbandry – the hamster; pp. 40–49.

Hoffman, R. A. (1968) Hibernation and the effects of low temperature. In R. A. Hoffman, P. F. Robinson & H. Magalhaes (eds.), *The golden hamster – its biology and use medical research*. Ames: Iowa State University Press. pp. 25–41.

Hoover, W. H., Mannings, C. L., & Sheerin, H. W. (1969) Observations on digestion in the golden hamster. *Journal of Animal Science 28*, 349–352.

Kent, G. C. (1968) The physiology of reproduction. In R. A. Hoffman, P. F. Robinson & H. Magalhaes (eds.), *The golden hamster – its biology and use medical research*. Ames: Iowa State University Press. pp. 119–139.

Lipman, N.S., & Foltz, C. (1996) Hamsters. In K. Laber-Laird, M. M. Swindle & P. Flecknell (eds.), *Handbook of rodent and rabbit medicine*. Oxford: Pergamon. pp. 59–91.

Magalhaes, H. (1968) Gross Anatomy. In R. A. Hoffman, P. F. Robinson & H. Magalhaes (eds.), *The golden hamster – its biology and use medical research*. Ames: Iowa State University Press. pp. 91–111.

McClure, D.E. (1999) Clinical pathology and sample collection in the laboratory rodent. In D. R. Reavill (ed.), *Clinical pathology and sample collection*. The veterinary clinics of North America: Exotic animal practice. Vol. 2. Philadelphia: WB Saunders. pp. 565–590.

Newcomer, C. E., Fitts, D. A., Goldman, B. D., Murphy, M.R., Rao, G.N., Shklar, G., & Schwartz, J.L. (1987) Experimental biology: Other research uses of Syrian hamsters. In G. L. Van Hoosier & C. A. W. McPherson (eds.), *Laboratory hamsters*. Orlando, Fla.: Academic Press. pp. 263–300.

Nowak, R. M. (ed.) (1999) Golden hamsters. *Walker's Mammals of the World*, 6th edn. Vol. 11. Baltimore: John Hopkins University Press. pp. 1423–1425.

Popesko, P., Rajtova, V., & Horak, J. (1992) *A colour atlas of anatomy of small laboratory animals*. Vol. 2. Aylesbury, UK: Wolfe. Rat, mouse, hamster; pp. 169–238.

Vaughan, T. A. (ed.) (1986) *Mammology*, 3rd edn. Philadelphia: Saunders College. Order Rodentia; pp. 244–277.

Whittaker, D. (1999) Hamsters. In T. Poole (ed.), *The UFAW handbook on the care and management of laboratory animals*, 7th edn. Vol. 1. pp. 356–366.

12

Ferrets

John Lewington

INTRODUCTION

Ferrets belong to the family Mustelidae, a diverse group of small to medium-size carnivores that includes weasels, stoats, polecats, mink, skunks, otters, and badgers. The ferret (*Mustela putorius furo*) is a domesticated polecat. The European polecat (*M. putorius putorius*) was probably the ancestor, but there is some argument about whether the domesticated ferret is derived from the European, Asiatic, Siberian or Ethiopian polecat.

Domestic ferrets have been used since Roman times to control rabbits by "ferreting", which continues today in Europe and Australia. While being working animals, used for controlling rabbits and rats, ferrets are also pets and kept as such in America, Britain, Europe, Australia, New Zealand, and Japan. Ferrets are also used as an experimental model for medical research and formerly for the fur trade. The study of ferret physiology was carried out initially in respect to ferrets' use for biomedical research (Whary & Andrews 1998). Evans and An (1998) have also extensively reviewed the complete anatomy of the ferret.

GENERAL EXTERNAL ANATOMY

The domestic ferret can be dark coated and dark eyed: the sable, "fitch-ferret" or "polecat-ferret," in contrast to the albino (pink-eyed white) ferret, which is the other traditional color. It has not been proved that the dark (sable) ferret is a product of a European polecat and white ferret mating (Owen 1984).

The base of the ferret head is narrower than that of the polecat; when viewed from above it resembles an isosceles triangle while the face of the polecat makes an equilateral triangle. The sable ferret's face is interesting for its panda mask appearance. It is similar to the European polecat, having dark eyes ringed with brown hair and then cream-colored hair between the eyes and ears, and between the eyes and nose. The eyes are characteristically less prominent than in the native polecat. The nose is white, mottled with brown, and the ears are small and set close to the head. Ferrets rely extensively on their sense of smell, even though they have efficient eyes and ears and typical cat-like tactile whiskers. Frances Pitt summed up the similarity of the ferret and polecat thus: "the 'fitch' ferret bears in outward appearance the same relation to the polecat that a half-printed photograph bears to a fully printed one from the same negative" (Pitt 1921).

Ferrets can live for 6 to 10 years and reach sexual maturity at 6 to 9 months of age. The hobs (males) are more otter-like in shape and size whereas the smaller jills (females) are more weasel-like. The ferret has short legs with an elongated body. It stands with an arched back and is agile in movement, further arching its back when running. The adult hob ferret body length (including tail) averages 38 cm; the ferret jill is typically shorter at around 35 cm. Ferret hobs weigh 1000 to 2000 g and ferret jills 600 to 900 g. The diploid chromosome number is 40.

SKELETAL SYSTEM

The vertebral formula is: C7, T15, L5 (6), S3, Cd 18 (Fig. 12.1). The ferret spine is very flexible, as befits an agile animal whose ancestor, the polecat, ranks among the most efficient of hunters. The ferret can turn around in a pipe or rabbit burrow in its own length and come racing out.

The ferret chest is very large compared to its body size. This is said to relate to the ancestry of the polecat as a slim, active hunter with useful increased lung capacity. The ferret has 15 pairs of ribs with the first 12 pairs attached to the sternum. The last five ribs make up the costal arch. The first ribs are relatively small, as are the last two, making the thoracic inlet narrow in contrast to other animals for the passage of the trachea, esophagus and large blood vessels. This can be significant when discussing chest problems.

The spinal cord can be subject to damage resulting from fractured vertebrae or disc protrusion. This is a particular risk in breeding jills, especially in a heavily pregnant or lactating jill when trying to clamber over some high object. Heavily-

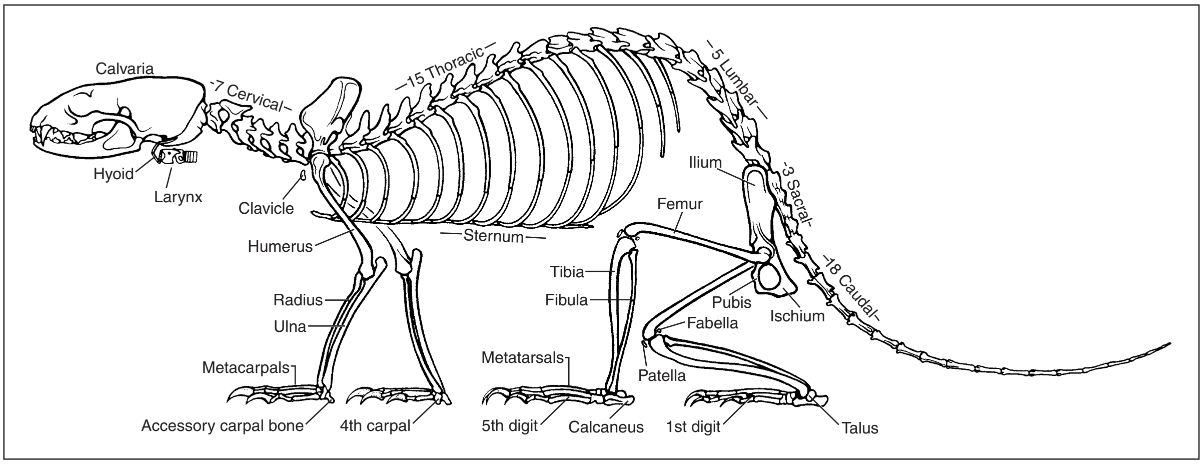


Figure 12.1 • The ferret skeleton. (Courtesy of Howard Evans.)

pregnant jills and heavy hobs should be well-supported by a hand under the rump when handling, to guard against excessive strain on the vertebral column.

The appendicular skeleton is naturally fine, light bone with long bones of matchstick diameter. In accident situations the long bones may fracture and require pinning with K-wire. It is also possible to use the femur for intraosseous blood transfusion. The ferret resembles the dog in having five toes with non-retractable claws, which in the house pet may require clipping.

Skull

The ferret skull shows the characteristics of the carnivore and it can be noted from Figure 12.2 that the ferret and dog have unclosed zygomatic bones to the eye orbit, in contrast to the cat (Wen et al. 1985). It can be seen from Figure 12.3a that one third of the ferret skull represents the short facial region and that the brain case is relatively large. Smith (1982) discovered that Australian ferrets had about two thirds the brain size of polecats.

CARDIOVASCULAR SYSTEM

Heart

The 4-chambered heart consists of left and right auricles and left and right ventricles, as is usual in mammals. The heart muscle is typical and, like the lungs, the ferret heart has been used in research (Whary & Andrews 1998). It lies between the 6th and 8th ribs and is obliquely placed in the thoracic cavity with the apex to the left side (Fig. 12.4). For auscultation purposes it lies more caudal in the chest than first imagined. The heart ligament joining it to the sternum will lose its fatty coat in cases of heart disease and, on radiology, if the heart is actually resting on the sternum, it can be a sign of early cardiac enlargement and disease according to Brown (1997).

It has been said that the unpaired innominate artery (brachiocephalic) at the base of the neck aids the ferret's agility (Willis & Barrow 1971) but there are still two common carotid arteries in the neck and not a single one as implied.

In the ferret the heart can be compromised with the occurrence of dilated cardiomyopathy (DCM) and hypertropic cardiomyopathy (HCM) in both sexes (Fig. 12.5). DCM progresses slowly over time whereas HCM initiates sudden death by left ventricle hypertrophy. The ferret heart can also become dysfunctional due to the presence of *Dirofilaria immitis* adults in the chambers, as with other carnivores.

Being a small mammal the ferret heart rate is usually between 200 and 400 beats per min. The cardiovascular/respiratory and arterial blood pressure standards are given in Table 12.1.

It is difficult to assess cardiac performance in the ferret using techniques such as systemic arterial blood pressure, central venous pressure, right ventricular pressure or pulmonary capillary wedge pressure. Estimations of cardiovascular performance, and more specifically, cardiac output, are usually limited to monitoring pulse strength and urine output. Unfortunately, the pulse is not reliably palpable in ferrets so urine output is therefore the best indicator of cardiac output (Lucas 2000).

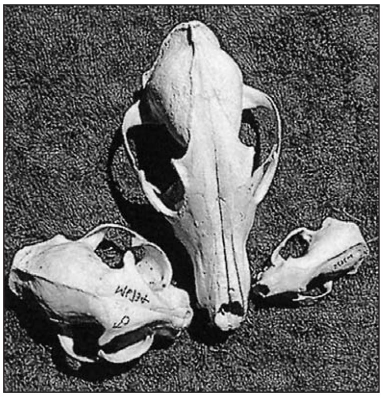


Figure 12.2 • Comparative skulls of three pet carnivores: ferret, dog, and cat.

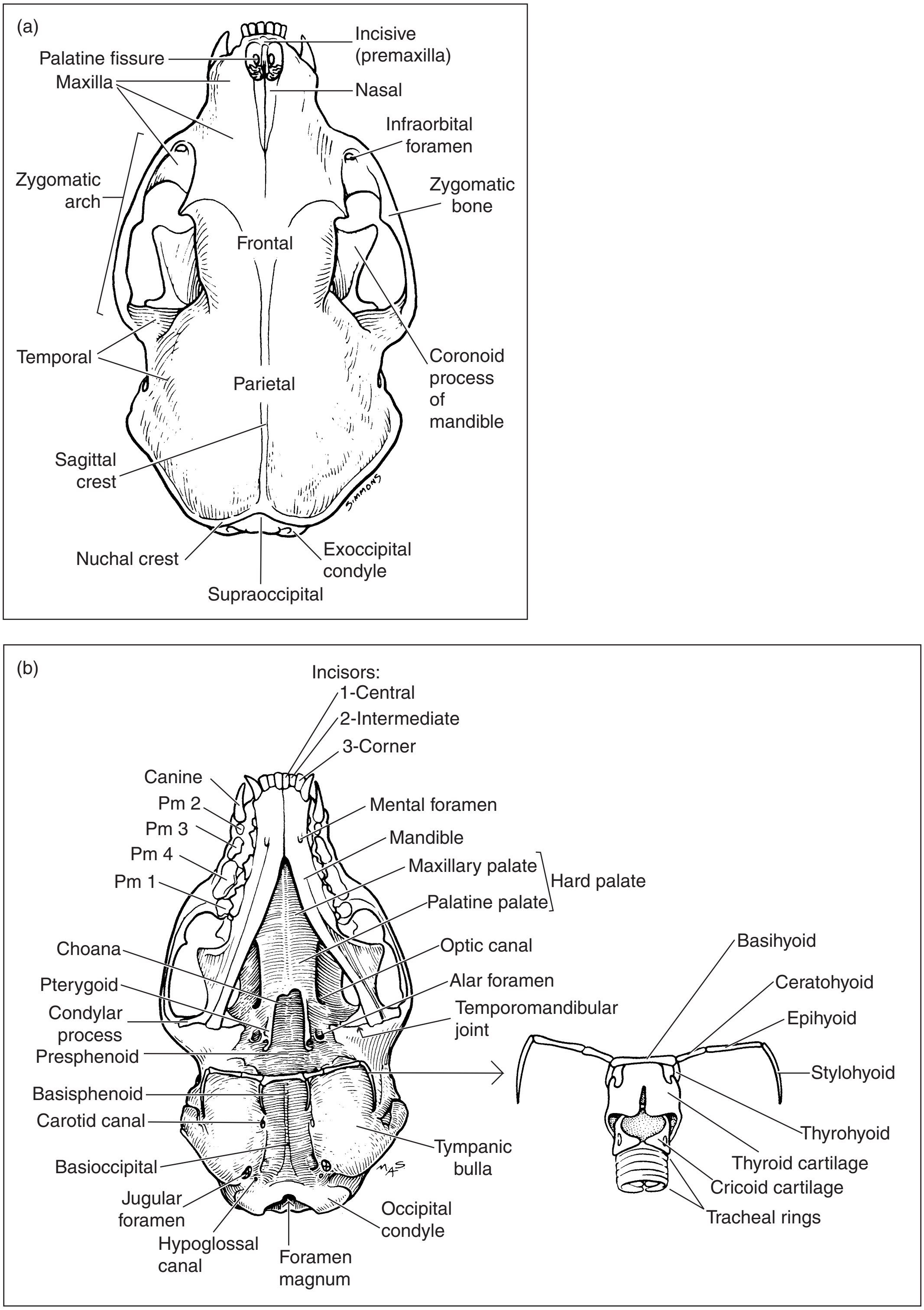

(a)
Palatine fissure
Maxilla
Incisive (premaxilla)
Nasal
Infraorbital foramen
Zygomatic arch
Zygomatic bone
Frontal
Temporal
Parietal
Coronoid process of mandible
Sagittal crest
SIMMONS
Nuchal crest
Exoccipital condyle
Supraoccipital
(b)
Incisors:
1-Central
2-Intermediate
3-Corner
Canine
Pm 2
Pm 3
Pm 4
Pm 1
Mental foramen
Mandible
Maxillary palate
Palatine palate
Hard palate
Choana
Optic canal
Pterygoid
Alar foramen
Condylar process
Temporomandibular joint
Presphenoid
Basisphenoid
Carotid canal
Basioccipital
Tympanic bulla
MAS
Jugular foramen
Hypoglossal canal
Foramen magnum
Occipital condyle
Basihyoid
Ceratohyoid
Epihyoid
Stylohyoid
Thyrohyoid
Thyroid cartilage
Cricoid cartilage
Tracheal rings

Figure 12.3 • (a) The ferret skull dorsal view, (b) The ferret skull ventral view. (Courtesy of Howard Evans.)

Venepuncture

Hematological and serum chemistry require venous blood sampling, using cephalic and jugular veins (Figs. 12.6 and 12.7). If you refer to Fig. 12.10, this also shows the external jugular vein, one of the main routes for bleeding or giving blood. It lies quite lateral on the neck and can be difficult to palpate in the hob due to its thickened neck. There is a laboratory technique for tail artery sampling, which is useful for periodic sampling of numerous ferrets (Curl & Curl 1985).

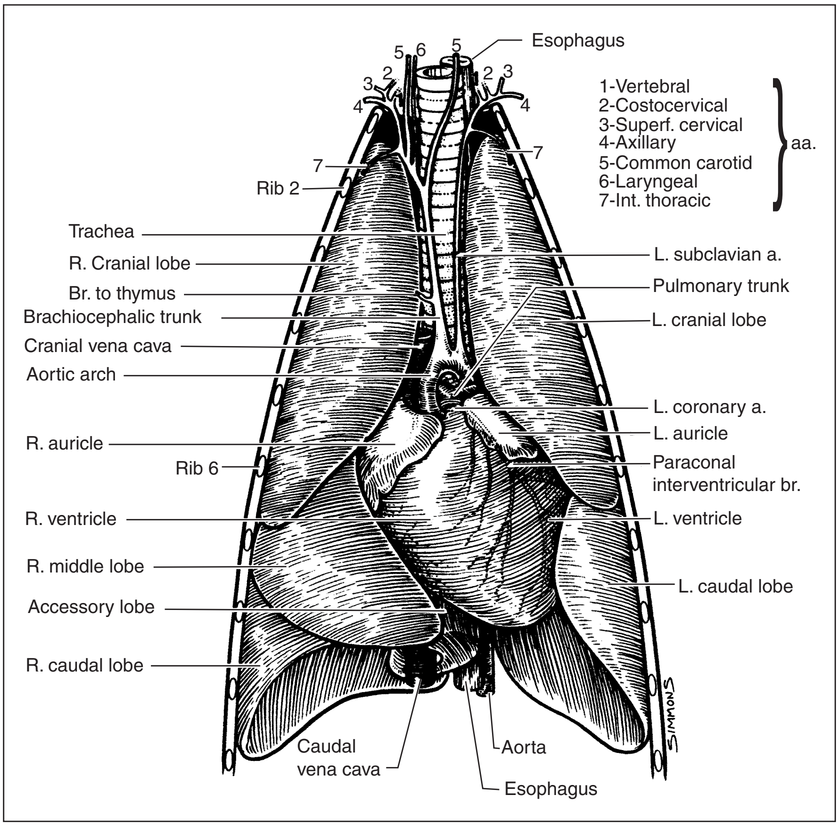

5 6 5
Esophagus
3 2 2 3
4 4
7 7
Rib 2
1-Vertebral
2-Costocervical
3-Superf. cervical
4-Axillary
5-Common carotid
6-Laryngeal
7-Int. thoracic
aa.
Trachea
R. Cranial lobe
Br. to thymus
Brachiocephalic trunk
Cranial vena cava
Aortic arch
R. auricle
Rib 6
R. ventricle
R. middle lobe
Accessory lobe
R. caudal lobe
L. subclavian a.
Pulmonary trunk
L. cranial lobe
L. coronary a.
L. auricle
Paraconal interventricular br.
L. ventricle
L. caudal lobe
Caudal vena cava
Aorta
Esophagus
SIMMONS

Figure 12.4 • Ferret heart and lungs (ventral view). (Courtesy of Howard Evans.)

The healthy ferret should have a packed cell volume (PCV) greater than 20%. For a sick ferret, with PCV below 15%, a blood transfusion is advised. Blood typing is not necessary in ferrets for blood transfusions (Manning & Bell 1990). Samples of 6, 9 or 12 ml of blood can be taken from jills, small or large hobs, respectively (Lucas 2000). Note that, when sedated, an average 1.5–2.0 kg hob can give 15–20 ml of blood and the average 0.75–1.00 kg jill, 10–12 ml (Jenkins & Brown 1993).

RESPIRATORY SYSTEM

Lungs

The lungs are relatively long in the tube-like space of the chest in such a sleek animal as the ferret. They give lateral and dorsal cover to the heart and are divided into cranial, middle, caudal, and accessory lobes on the right side, and cranial and caudal on the left (Fig. 12.4). The thoracic inlet

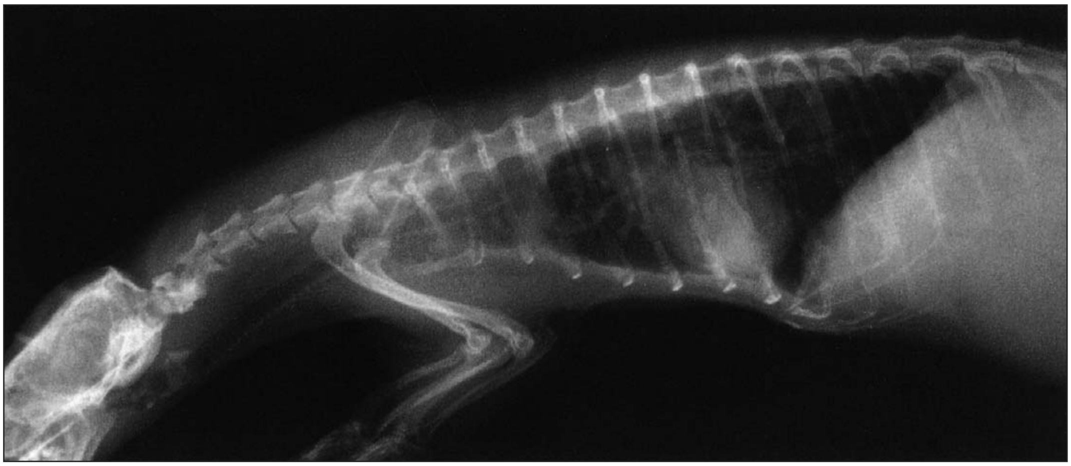


Figure 12.5 • Radiograph of ferret showing chest structure. This ferret has cardiomyopathy.

Table 12.1 Cardiovascular / respiratory and arterial blood pressure standard measurements

Mean systolic	Jill 133, hob 161 mmHg (conscious)
Mean diastolic	110–125 mmHg (anesthetized)
Heart rate	200–400 beats/min
Cardiac output	139 ml/min
Circulation time	4.5–6.8 s
Blood volume	Jill 40 ml, hob 60 ml (5–7% of body weight)
Respiration	33–36/min
Body temperature	38.8° C (range 37.8–40° C).

Adapted from Fox, J. G. (1988). *Biology and diseases of the ferret*, 2nd edn. p. 184, with permission

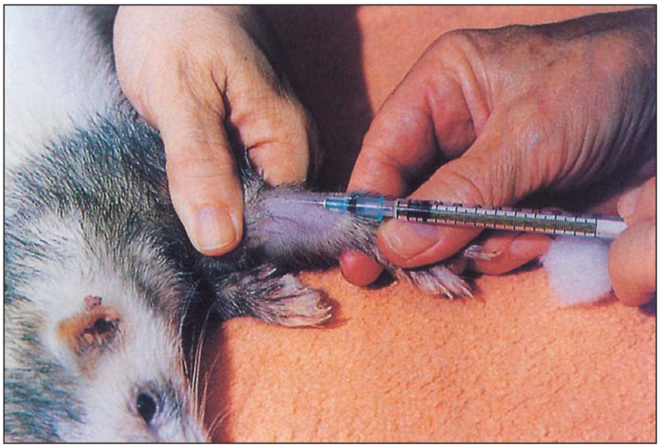


Figure 12.6 • Taking blood from the cephalic vein. Photo courtesy of John Tingay.

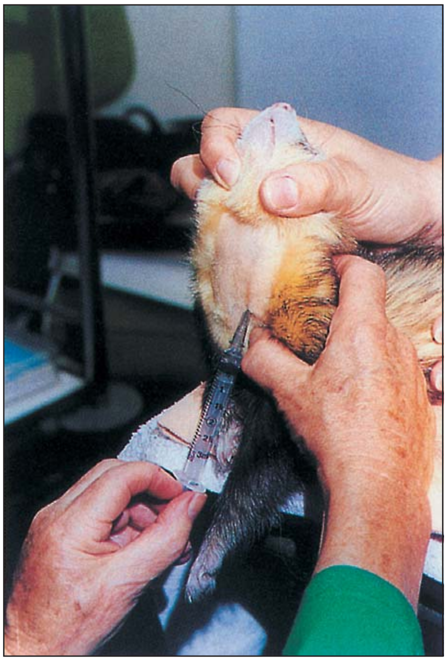


Figure 12.7 • Taking blood from the jugular vein. Photo courtesy of John Tingay.

is narrower compared to other carnivores which have more bulk, such as dogs, and contains anterior mediastinal lymph nodes and passage of the trachea, esophagus, and major blood vessels. Any abnormality of even one organ at this point can cause serious interference with chest function. Major neoplastic conditions can arise in young and old ferrets, such as lymphoma and fibrosarcoma.

The ferret lungs have a large volume in relation to body weight, with the total lung capacity exceeding a predicted value by 297%, hence their value as experimental animals for research into human conditions. Interestingly, ferret lung structure contains excess submucosal glands in the bronchial wall and extra terminal bronchioles, making them anatomically like human lungs (Whary & Andrews 1998). Ferrets can be infected with human influenza virus as well as canine distemper.

CLINICAL NOTE

During operations care must be taken not to compress the ferret's chest as they rely more on diaphragm movement for ventilation under anesthesia than on costal movement. If a ferret stops breathing, cardiopulmonary resuscitation can be instigated by holding it by the legs and moving it side to side to stimulate diaphragmatic breathing.

DIGESTIVE SYSTEM

Dentition

Adult ferrets have typical carnivore dentition with large curved canines and strong premolars and molars (Figs. 12.3b and 12.9).

Deciduous dentition

(Pass et al. 1993)

Upper Arcade	I	4	4	C	1	1	P	3	3	M	0	0
Lower	I	3	3	C	1	1	P	3	3	M	0	0

Total 30 teeth

CLINICAL NOTE

The kitten's temporary teeth first erupt between the 3rd and 4th week so it is possible for needle-sharp canines to inflict damage on the jill's mammary glands, leading to mastitis.

Permanent dentition

(Pass et al. 1993)

Upper Arcade	I	3	3	C	1	1	P	3	3	M	1	1
Lower	I	3	3	C	1	1	P	3	3	M	2	2

Total 34 teeth

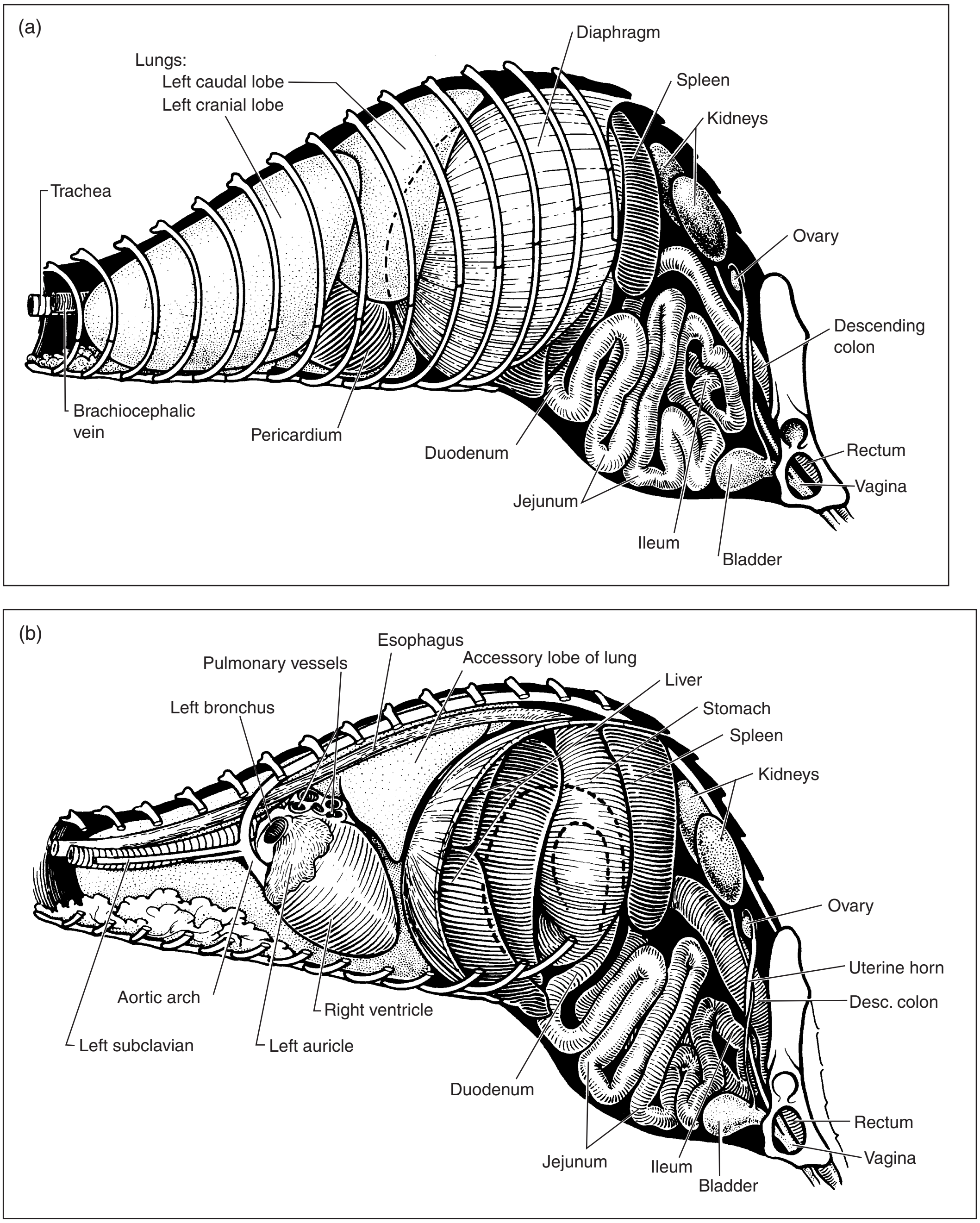

(a)
Diaphragm
Lungs:
Left caudal lobe
Left cranial lobe
Spleen
Kidneys
Trachea
Ovary
Descending colon
Brachiocephalic vein
Pericardium
Duodenum
Rectum
Vagina
Jejunum
Ileum
Bladder
(b)
Esophagus
Pulmonary vessels
Accessory lobe of lung
Liver
Left bronchus
Stomach
Spleen
Kidneys
Ovary
Uterine horn
Desc. colon
Aortic arch
Right ventricle
Left subclavian
Left auricle
Duodenum
Rectum
Jejunum
Ileum
Vagina
Bladder

Figure 12.8 • (a) The thoracic and abdominal viscera by a superficial left lateral view. The *dotted line* shows the curve of the diaphragm. (b) The ferret thoracic and abdominal viscera on lateral view showing left lung removed. The *dotted lines* show the stomach passing to the pylorus dorsally and the duodenum. (Courtesy of Howard Evans.)

The ferret's permanent teeth appear from the 7th week of age, with the upper and lower canines plus the first lower molar appearing first. At about 53 days the upper molar is seen. This is followed by the second, third, and fourth upper premolars and the second and third lower premolars, which are all present by 67 days after birth. Finally, in the lower jaw, the fourth premolar and second molar are present a week later (Evans & An 1998).

The rostral view of the adult ferret skull (Fig. 12.9) illustrates the very narrow ventral space in the nasal conchae, through which only a 3.0 or 3.5 French red rubber catheter could be passed in an emergency.

The ferret or polecat jaw is powerful enough to kill small prey by crushing the skull, using the biting canines. A well-adjusted pet ferret is unlikely to bite to hurt unless alarmed or in pain. Young ferrets may nip in the process of "play-fighting," either with each other or with their owner, but the skin is not usually penetrated.

Abnormalities can occur in the dentition. Western Australian ferret kittens have shown supernumerary incisors. In one

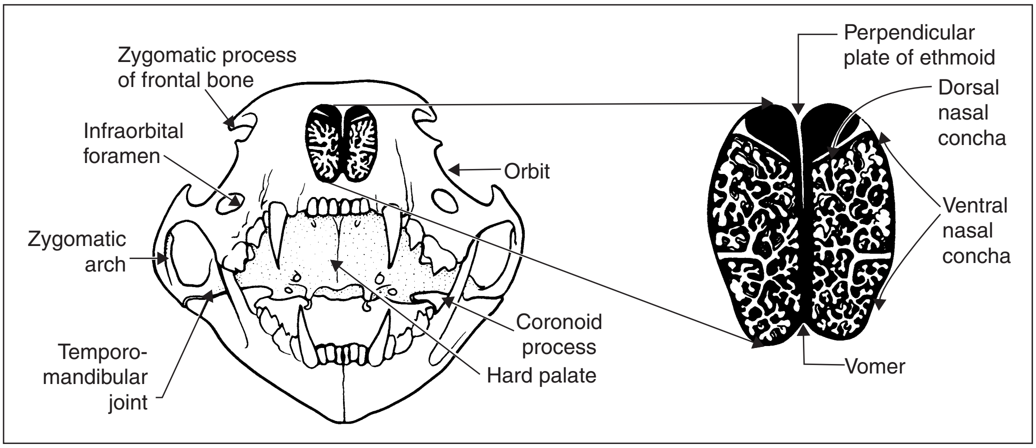

Zygomatic process of frontal bone
Infraorbital foramen
Zygomatic arch
Temporo-mandibular joint
Orbit
Coronoid process
Hard palate
Perpendicular plate of ethmoid
Dorsal nasal concha
Ventral nasal concha
Vomer

Figure 12.9 • Ferret skull (rostral view). (Courtesy of Howard Evans.)

survey of 350 ferrets from various UK breeders, 26 ferrets had one or two supernumerary incisors (Andrews et al. 1979). There were three ferrets with broken canines. This was considered at the time an action by ferreters to stop them killing rabbits, but it is not necessary and today would be regarded as a mutilation. Canine teeth can be fractured in fights or by accidents, and modern ferret dentistry can effect a repair (Johnson-Delaney & Nelson 1992). Basic dentistry is commonly carried out for scaling and extracting teeth under anesthesia with pet ferrets, as with dogs and cats.

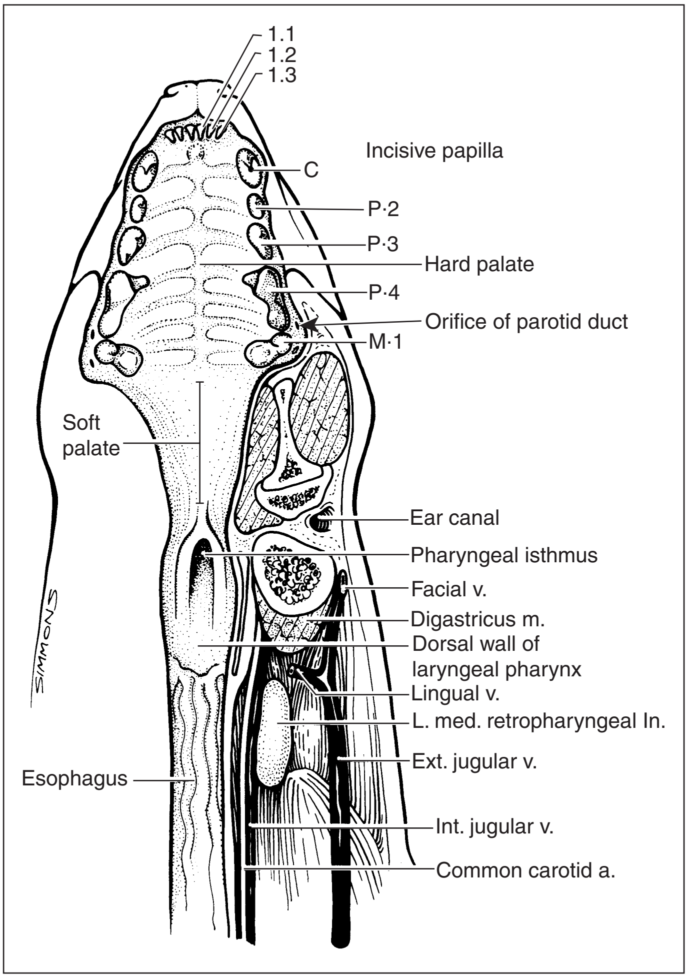

1.1
1.2
1.3
Incisive papilla
C
P·2
P·3
Hard palate
P·4
Orifice of parotid duct
M·1
Soft palate
Ear canal
Pharyngeal isthmus
Facial v.
Digastricus m.
Dorsal wall of laryngeal pharynx
Lingual v.
L. med. retropharyngeal ln.
Ext. jugular v.
Esophagus
Int. jugular v.
Common carotid a.
SIMMONS

Figure 12.10 • Ferret pharynx and structures of interest. (Courtesy of Howard Evans.)

CLINICAL NOTE

In the upper dental arcade the first molar appears tucked behind the fourth premolar and is sometimes the site of a root abscess.

Muscles of mastication

The well-developed masseter muscle originates at the zygomatic arch and inserts on the masseteric fossa, condyloid crest, and mandibular angular process. The digastric muscle originates on the jugular process and tympanic bulla and passes to the ventral border of the caudal portion of the mandible and has the action of opening the jaw. The major adductor muscle of the lower jaw is the temporalis and this is well developed in the hob. The deep pterygoid muscles, lateral and medial, assist the masseter and temporalis muscles in the crushing and chewing motion of closing the jaws.

GENERAL INTEREST

The ferret has a powerful bite and can clamp its jaws tight on prey and will not let go. Large strong birds, which have been bitten on the foot, have been known to take weasels, stoats and even polecats aloft!

Tongue

The ferret tongue (Fig. 12.11) is long and freely movable and can be pulled forward to expose the tracheal entrance for endotracheal tubing, as in other mammals. The lingual frenulum can be the site of grass awn penetrations, especially in working ferrets in summer.

Salivary glands

The ferret has five pairs of salivary glands: parotid, mandibular, sublingual, molar, and zygomatic (Fig. 12.12). These glands can be damaged in fights between hob ferrets, typically in the mating season. The resulting formation of mucoceles will require surgical drainage. Miller and Pickett (1989) have described an operation on a zygomatic salivary gland mucocele.

Gastrointestinal tract

The esophagus can have a dilated transthoracic section, defined as a megaesophagus, which is sometimes also seen in puppies. This condition has occurred in ferrets but is now a rarity. The musculature of the esophagus is thin and weak and motility is reduced, leading to typical food bolus collection and regurgitation. Ferrets are able to vomit and have been used in experiments on the physiology of vomiting relating to humans.

The ferret has a short digestive tract like other carnivores, with a simple stomach lying on the curve of the liver in the cranial abdomen (Figs. 12.8a, b and 12.13). The stomach is capable of tremendous swelling and an adult hob ferret has been known to eat 80 g of meat at one time and then slowly digest it overnight.

Intestines

The small intestine is approximately 182–198 cm long and extends from the pylorus of the stomach to the junction with the colon (Evans & An 1998)(Figs. 12.13 and 12.14). The duodenum, the proximal loop of small intestine, is about 10 cm long. The ileum and jejunum have no apparent demarcation and pass to the large intestine, which is approximately 10 cm long. There is no ileocolonic valve in the ferret and no cecum or appendix. Because the cecum is missing, the ileocecal

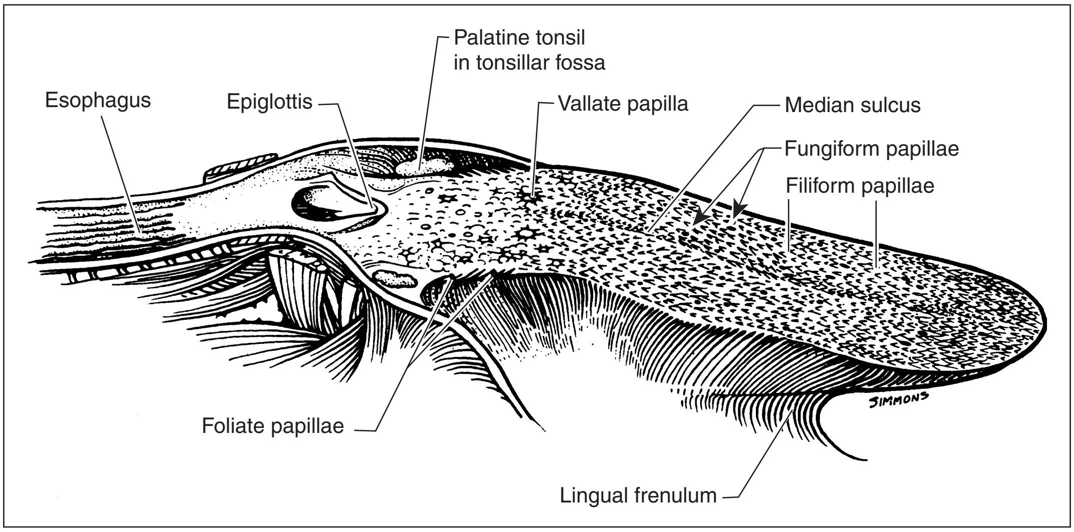


Figure 12.11 • The ferret tongue. (Courtesy of Howard Evans.)

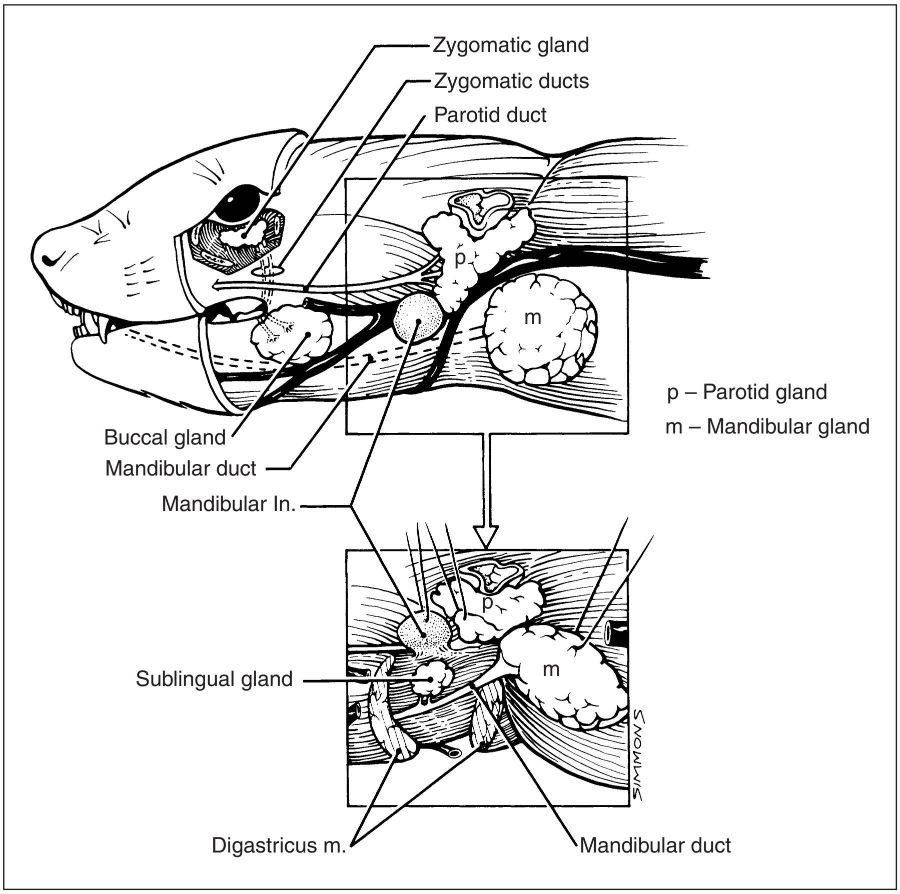


Figure 12.12 • Ferret salivary glands. (Courtesy of Howard Evans.)

junction is indistinct; however, the junction can be inferred by the pattern of the jejunal artery, which anastomoses with the ileocecal artery. The colon is divided into ascending, transverse, and descending portions and ends at the junction with the rectum at the pelvic inlet level (Evans & An 1998). The bowel is subject to obstructions: for example, chewed plastic toys. Foreign body operation procedure has been described (Bennett & Pye 2000).

The anus has an internal (smooth muscle) and external (voluntary muscle) sphincter system (Evans & An 1998). The external sphincter encloses the paired musk glands, which have openings on either side of the anal canal (Fig. 12.18). The musk glands are approximately 10 mm by 5 mm and their removal (anal sacculectomy) has been described (Bennett & Pye 2000).

Liver

The diaphragm itself is divided into a typical muscular dome with central tendinous area and two crura. The liver fits into the mould of the ferret diaphragm and is relatively large compared to the average ferret body weight; an 800–1150 g animal could have a liver of 35–59 g (Evans & An 1998). The liver has right lateral, right, and left medial lobes, a quadrate central lobe hiding the gall bladder, and a left lateral lobe, all in the curvature of the diaphragm (Fig. 12.15). The liver can be the site of primary neoplasia or subject to secondary invasions of malignant cells.

Pancreas and spleen

The pancreas is an elongate, lobulate, inverted ‘V’-shaped organ, usually light pink to bright red in color (Figs. 12.14 and 12.15). It can be the site of insulinoma cancers in ferrets. Delicate surgery for pancreatic beta-cell tumors has been described (Bennett & Pye 2000).

The spleen is a gray-brown organ lying in the left hypogastric area, running parallel to the greater curvature of the stomach. It is crescent shaped and can become large quite normally in adults, though also very enlarged as a primary or secondary cancer.

KEY POINTS

- The ferret skeleton is lightweight but extremely flexible and strong.
- The thoracic cavity is large relative to body size.
- Ferrets have no ileocolonic valve, cecum, or appendix.

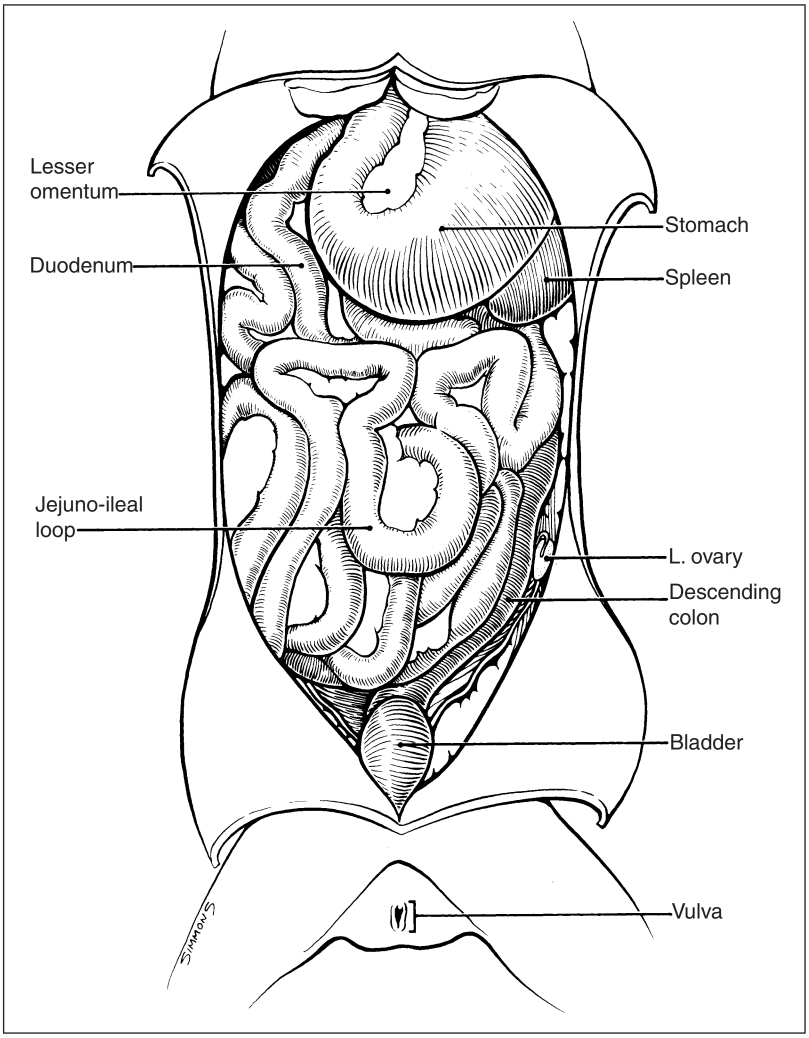


Figure 12.13 • Ferret internal viscera – undisturbed as for an abdominal operation. (Courtesy of Howard Evans.)

URINARY SYSTEM

The urinary organs function as with all mammals to remove waste products from the blood circulation, and any dysfunction can be life-threatening.

Kidneys

The kidneys are both retroperitoneal, lying in the sublumbar region on either side of the vertebral column, main aorta, and caudal vena cava (Fig. 12.16). They have a typical bean shape. They are typically mammalian with the usual cortical and medullary areas around the pelvis of the ureter. However, the autonomic nerve supply is more complicated than in other species (Whary & Andrews 1998).

Serum chemistry in ferrets differs from dogs and cats in that the serum creatinine findings do not parallel elevations in the blood urea nitrogen (BUN) in renal failure (Hillyer 1997). Later estimations of glomerular function rate decided that using serum BUN and creatinine readings to determine renal insufficiency are questionable as the BUN can be influenced by non-renal factors. It is stated that the increase in serum concentrations of both substances do not actually appear until the kidney is 75% damaged (Esteves et al. 1994). It has been considered that creatinine elevation for ferrets is much lower than that of dogs and cats, as the normal mean value is lower (0.4–0.6 mg/dL) and the range is narrower (0.2–0.9 mg/dL). It may be that renal tubular secretion or enteric factors may be more prominent in affecting creatinine metabolism in ferrets than other animals (Rosenthal 1994). For laboratory ferrets with a food consumption of 140–190 g per 24 hrs, and a water intake of 75–100 ml per 24 hours, the urine volume is put at 26–28 ml per 24 hours with a urine pH of 6.5–7.5 (Fox 1998).

Enlargement of one or both kidneys has been recorded in the USA in ferrets over 3 years of age (Fox et al. 1998; Jenkins & Brown 1993). The condition can be associated, not with infection, but with renal cysts (Fig. 12.17). These can be single or multiple cysts and are considered to be hereditary, developmental or acquired (Dillberger 1995), usually with no clinical signs, or perhaps associated with renal failure (Rosenthal 1994). Acute and chronic renal failure, other

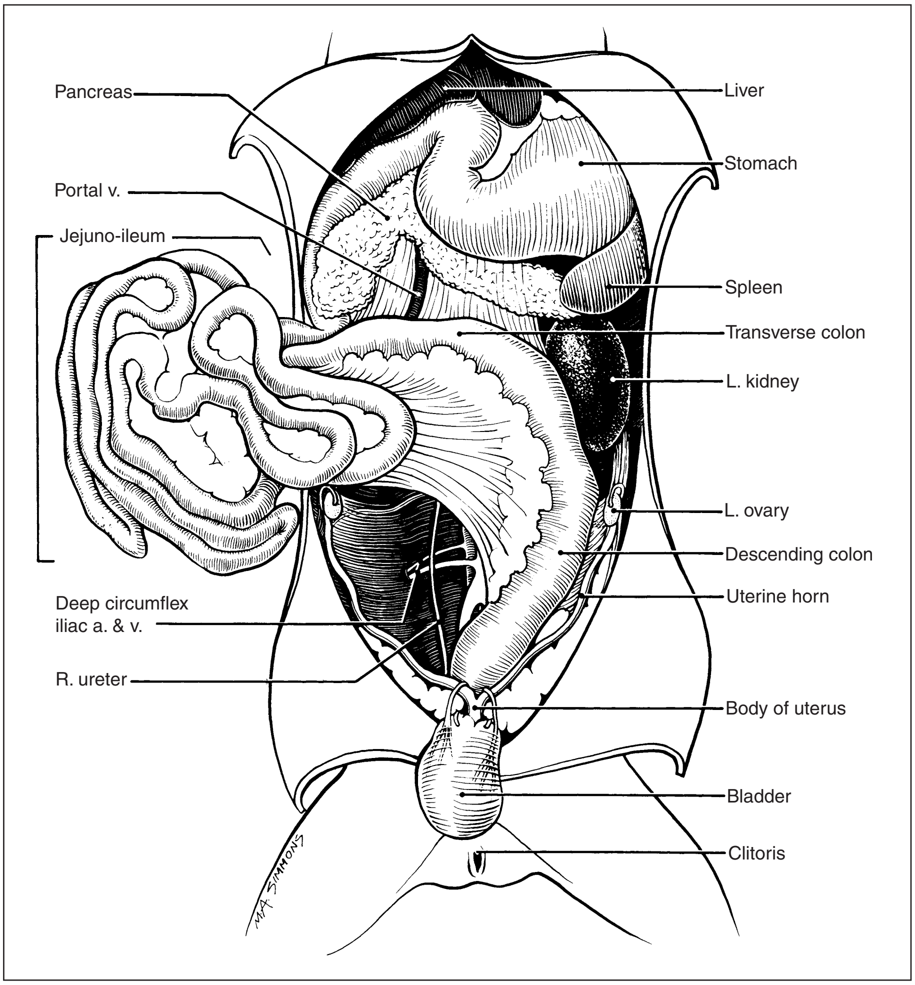

Pancreas
Portal v.
Jejuno-ileum
Deep circumflex iliac a. & v.
R. ureter
Liver
Stomach
Spleen
Transverse colon
L. kidney
L. ovary
Descending colon
Uterine horn
Body of uterus
Bladder
Clitoris
M.A. SIMMONS

Figure 12.14 • Ferret abdominal viscera with intestines displaced. (Courtesy of Howard Evans.)

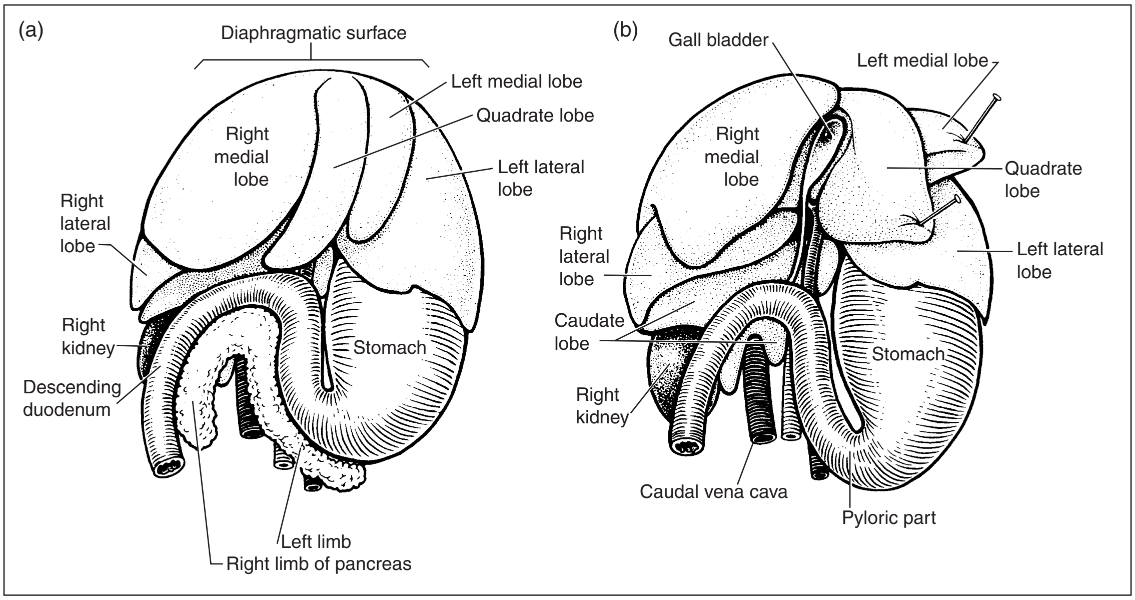

(a)
Diaphragmatic surface
Left medial lobe
Quadrate lobe
Right medial lobe
Left lateral lobe
Right lateral lobe
Right kidney
Descending duodenum
Stomach
Left limb
Right limb of pancreas
(b)
Gall bladder
Left medial lobe
Right medial lobe
Quadrate lobe
Right lateral lobe
Left lateral lobe
Caudate lobe
Stomach
Right kidney
Caudal vena cava
Pyloric part

Figure 12.15 • (a) The liver showing organs in situ, (b) The liver reflected showing gall bladder and with pancreas removed. (Courtesy of Howard Evans.)

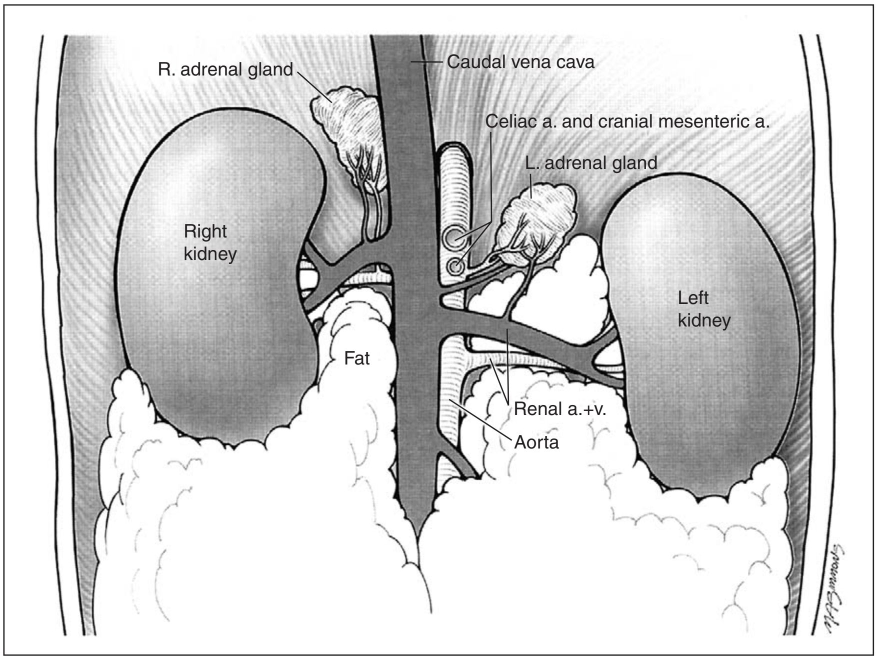


Figure 12.16 • Ferret adrenal glands and kidneys. (Courtesy of Lippincott Williams & Wilkins and Howard Evans.)

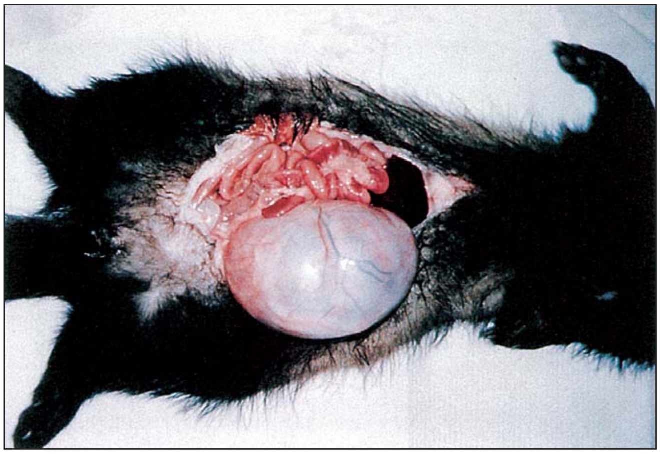


Figure 12.17 • Renal cyst in 3-month-old ferret. Slide courtesy of Dr. G. Rich.

than cystic kidneys, can occur as with other mammals and treatment has been described (Lewington 2003c).

Ureters

The delicate ureters run from the renal pelvis and enter the base of the bladder from the left and right side. In the male ferret they are affected by inflammation of the prostate when urinary outflow is restricted.

Bladder

The bladder naturally varies in size depending on contents but when empty measures roughly 1 cm wide by 2 cm long. In the adult it has the capacity of around 10 ml of urine.

Urine is used to mark territory by ferrets, as with other animals. An interesting point in bladder innervation is that sympathetic and parasympathetic nerves cause contraction of the whole bladder, while in other animals the sympathetic nerves produce relaxation (Whary & Andrews 1998).

CLINICAL NOTE

The bladder can be the site of cystic calculi, possibly due to commercial foods as it is not seen in ferrets fed fresh meat. Usually the condition is acute in males and chronic in females.

KEY NOTES

- The ferret has a large lung capacity relative to its size.
- Blood typing for transfusion between ferrets is not required as for other mammals.
- BUN and creatinine values differ from those in dogs and cats.

REPRODUCTIVE SYSTEM

Ferrets are sexually mature at 6–9 months of age and reproduce twice yearly with coitus-induced ovulation. Unmated jills can die from postestrus anemia. Gestation is 42 days; kitten birth weight is 10 g (range 8–12 g) with a litter size of 4 to 14, reducing with the age of the jill. Kittens can hear from 32 days and the eyes open at 4–5 weeks. They can be weaned at 6–8 weeks.

Dysfunction of the reproductive system can occur in the unsterilized jill (female) and the sterilized hob (male).

MALE

Testes

The ferret scrotum has two cavities, each of which houses a testis and epididymis (Figs. 12.18 ad 12.19a, b). The epididymis is composed of a mass of convoluted spermatic duct, which is divided into head, body, and tail on the dorsal aspect of the testis as it lies in the scrotal sac. The head of the epididymis receives the efferent ductules as they leave the testis at the cranial pole. The body of the epididymis has the main mass of the convoluting spermatic duct, which passes to the tail of the epididymis at the caudal pole of the testis. The spermatic duct becomes apparent as a simple duct to the tail of the epididymis and passes cranially on the dorsal aspect of the testes as the ductus deferens (vas deferens). It is medial to the body of the epididymis.

The ductus deferens is accompanied by the deferent artery and vein and the main testicular artery and vein, which, with the nerve and lymphatic system vessels, form the spermatic cord. It passes cranially to the inguinal passage into the abdomen where it then parts company with the testicular artery, looping over the urethra through the prostate gland.

Histologically, the testis, blood vessels, nerves, lymphatics, and ductus deferens are wrapped in a pouch of peritoneum called the vaginal sac. This sac extends through the inguinal canal in development prior to the descent of the testis.

Castration of hob ferrets is a common operation (Bennett & Pye 2000) but a more delicate and equally important operation is that of vasectomy (Lewington 2003c). The treated hob can then be used to take jills off heat, to rest them from breeding without recourse to hormonal injection.

During vasectomy surgery the common vaginal tunic of the spermatic cord must be delicately dissected open to expose the ductus deferens and avoid injury to the main testicular artery. The ductus deferens lies medial to the testicular artery and vein inside the spermatic cord (Lewington 2003g).

The hob genitalia resemble the dog in having an os penis or baculum. The os penis of the ferret, and indeed other mustelids, is a bony strengthening rod, as in the dog, but has an exterior curled point that makes urethral catheterization difficult. Despite the presence of the curled end, catheterization can be achieved using a 3.5 French catheter (Lucas 2000) (Fig. 12.20).

Prostate gland

The prostate is a glandular structure, which adds elements to the seminal fluid. It lies at the base of the bladder surrounding the urethra (Fig. 12.18). It is not very distinct in the young ferret. As it completely surrounds the urethra, inflammation of the gland will affect the urinary outflow. At the level of the prostate the ductus deferens from each side opens into the urethra.

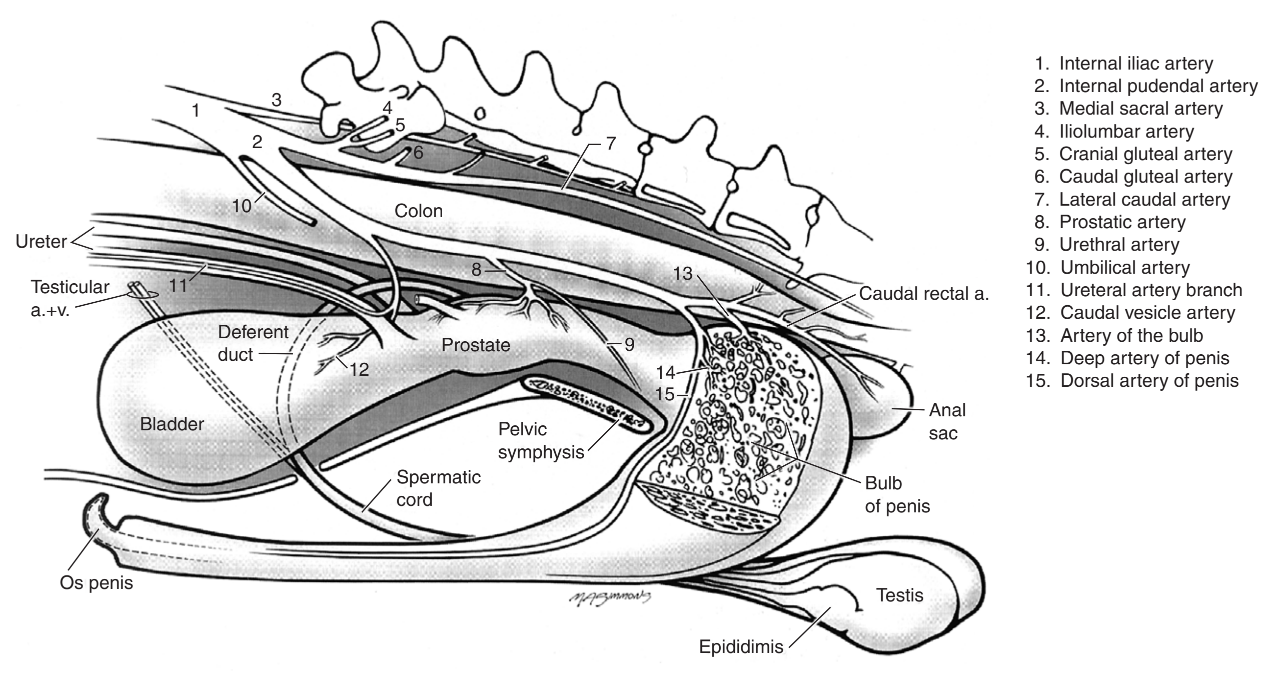

1
3
4
5
2
6
7
10
Colon
Ureter
8
13
Caudal rectal a.
Testicular a.+v.
11
Deferent duct
Prostate
9
12
14
15
Anal sac
Bladder
Pelvic symphysis
Spermatic cord
Bulb of penis
Os penis
Testis
Epididimis
1. Internal iliac artery
2. Internal pudendal artery
3. Medial sacral artery
4. Iliolumbar artery
5. Cranial gluteal artery
6. Caudal gluteal artery
7. Lateral caudal artery
8. Prostatic artery
9. Urethral artery
10. Umbilical artery
11. Ureteral artery branch
12. Caudal vesicle artery
13. Artery of the bulb
14. Deep artery of penis
15. Dorsal artery of penis

Figure 12.18 • **The bladder in relation to the hob reproductive system. (Courtesy of Lippincott Williams & Wilkins and Howard Evans.)**

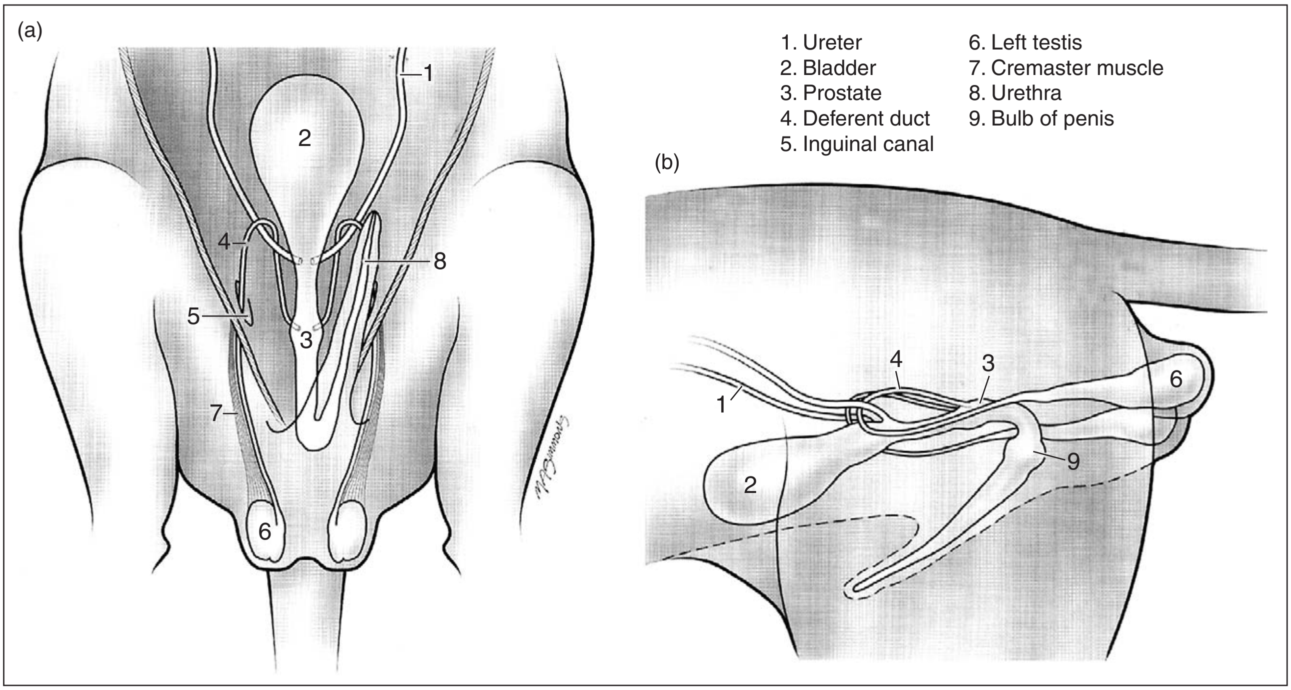


Figure 12.19 • (a) Hob genitalia ventral view; (b) Hob genitalia right lateral view. (Courtesy of Lippincott Williams & Wilkins and Howard Evans.)

Prostatic cysts can develop in association with adrenal gland neoplasia (AGN), which can cause urethral obstruction (Fig. 12.21). The gland becomes enlarged in mostly American sterilized hobs as a frequent complication of AGN. This is not a problem of unsterilized hobs or animals sterilized at a mature age but is common in American male ferrets, which are sterilized at 6 weeks (Jenkins & Brown 1993). Once adrenalectomy is carried out the prostate rapidly reduces in one to two days. Surgery can be performed on this condition (Bennett & Pye 2000).

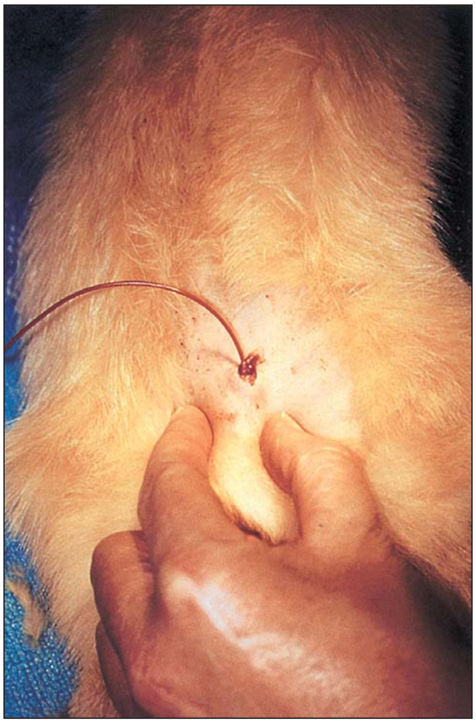


Figure 12.20 • Urethral catheterization of the hob ferret. Note the J-shaped os penis to the top right of the catheter. The urethra does not bend around inside the os penis. Slide courtesy of Dr. Anthony Lucas.

Female

Ovaries

The weight of an ovary is 94–183 mg in a 600–800 g ferret, with the average size being 0.45 cm long by 0.55 cm wide

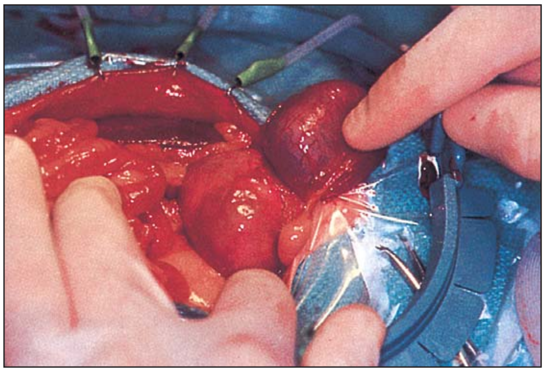


Figure 12.21 • Prostatic cyst in a ferret. The large prostatic cyst can be seen dorsal to the reflected and elevated bladder. Note the use of a stay retractor to facilitate exposure of the abdomen. The hooks of the stays have been placed in the muscle of the body wall. Slide courtesy of Prof. Avery Bennett.

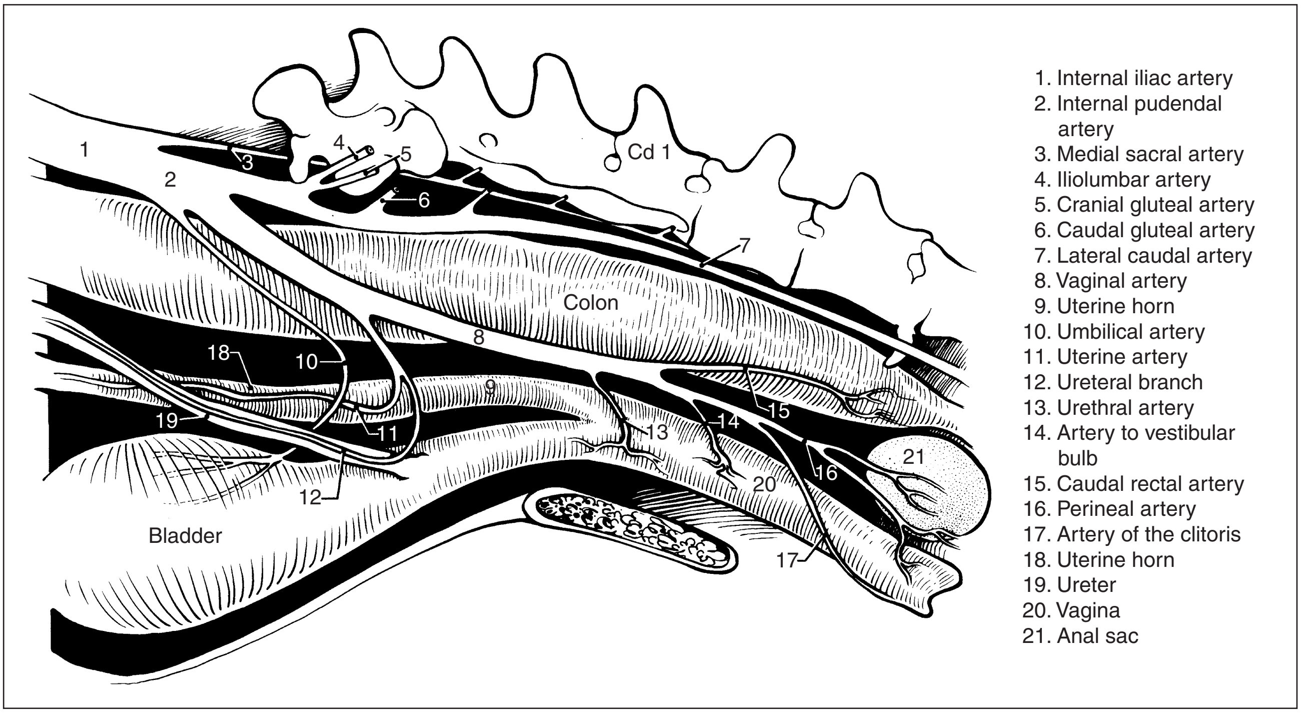

1
2
3
4
5
6
Cd 1
7
Colon
8
9
10
11
12
13
14
15
16
17
18
19
20
21
Bladder
1. Internal iliac artery
2. Internal pudendal artery
3. Medial sacral artery
4. Iliolumbar artery
5. Cranial gluteal artery
6. Caudal gluteal artery
7. Lateral caudal artery
8. Vaginal artery
9. Uterine horn
10. Umbilical artery
11. Uterine artery
12. Ureteral branch
13. Urethral artery
14. Artery to vestibular bulb
15. Caudal rectal artery
16. Perineal artery
17. Artery of the clitoris
18. Uterine horn
19. Ureter
20. Vagina
21. Anal sac

Figure 12.22 • The bladder in relation to the jill reproductive system. Courtesy of Howard Evans.

and 0.21 cm thick (Evans & An 1998). When mature, the left ovary lies caudal to the middle of the 14th rib and caudal to the left kidney. The right ovary is caudal to the middle of the last rib (15th) and also caudal to the right kidney. The ovaries are suspended by ligaments from the abdominal wall.

Uterus

The ferret uterus is bicornuate, comprising two long, tapering uterine horns that combine immediately in front of the cervix to form a short uterine body (Fig. 12.22). The mature uterine horns are about 4.3 cm long and 0.22 cm wide, while the body is 1.7 cm long and 0.25 cm wide (Evans & An 1998). Blood supply is by the companion ovarian and uterine arteries and veins (Fig. 12.25); sympathetic innervation comes from the aortic and renal plexuses.

Ovariohysterectomy is done as per the cat. The ovarian ligaments are loose and easily torn to exteriorize the ovaries.

CLINICAL NOTE

During spaying, the ovaries might well be obscured by the presence of fat and thus care must be taken in making sure the full ovary is removed, and no remnants are left, as these can produce hormonal problems.

Estrous cycle

The sexual cycle of the ferret comes with maturity at 6–9 months of age. Breeding is tuned to the increasing daylight periods in spring. Normally the vulva is hardly visible in the live animal, becoming red and swollen when the jill is in heat.

Ovulation is stimulated by coitus, with the jill becoming anestrus 1 week after fertilization. Failure of the jill to mate results in continuous hormonal stimulation of estrogen from the ovaries, leading to the dangerous condition of hyperestrogenism. The condition arising is postestrus anemia. The jill's vulva continues to be swollen, she becomes anemic, shows alopecia and is very sick (Fig. 12.23). The high blood estrogen from the active ovaries causes suppression of the bone marrow and a non-regenerative anemia with depression of PCV below 25%. If the PCV falls below 15% it is considered irreversible. Treatment is by immediate ovariohysterectomy if the PCV is still high or else blood transfusion and intensive care is required. In addition the uterus can develop pyometra as a result of ascending vaginal infections or as a sequel to postestrus anemia.

Thus the female ferret, unlike other mammals, must be mated, taken out of estrus by a vasectomized hob, or given chemical estrus suppression drugs (Lewington 2003c). Feral ferrets and other Mustelidae are usually kept mated in the season or die quickly. American pet ferrets do not get postestrus anemia as non-breeding jills are sterilized at 6 weeks of age; however they are plagued with adrenal gland neoplasia (AGN) and insulinoma, as shown later.

KEY NOTES

- Prostatitis occurs in the sterilized male, associated with adrenal gland neoplasia (AGN).
- The os penis has a curled end making catheterization difficult but not impossible.
- Postestrus anemia occurs in the unmated female during estrus.

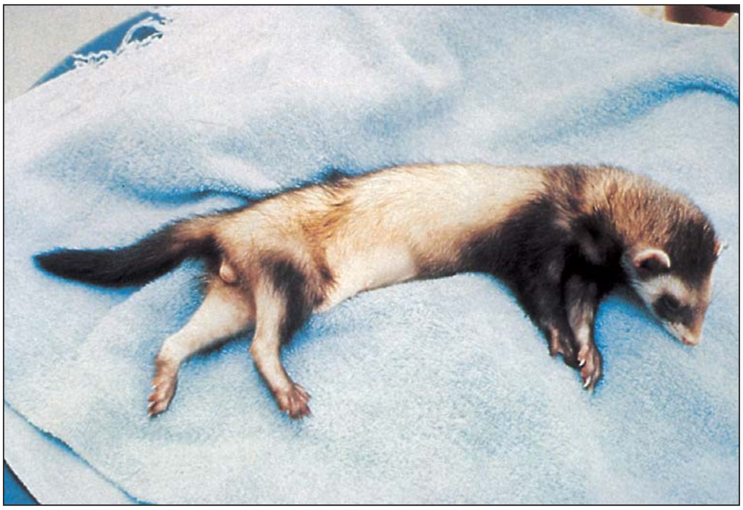


Figure 12.23 • Jill with postestrus anemia showing alopecia and swollen vulva. Slide courtesy of D. Manning, University of Wisconsin.

ENDOCRINE SYSTEM

Parathyroid and thyroid

Figure 12.24 provides a ventral view of the ferret head and neck region and shows the position of the thyroid and parathyroid glands plus the right medial retropharyngeal lymph node. The latter can be the site of neoplasia, as can other external lymph nodes. The ventral isthmus of the bilobed thyroid lies dorsal to the tracheal rings. The thyroid is darker than the pale parathyroid glands, which lie cranial to it along the trachea.

Adrenal glands

The adrenal glands and the pancreas have been sites of increasing numbers of neoplasia in ferrets in recent years.

The left and right adrenal glands (Fig. 12.16) are situated adjacent to the upper borders of the left and right kidneys and are usually embedded in fat. The exact positions vary with individual animals (Holmes 1961). Both adrenal glands are subject to hormone-stimulated neoplasia. The left adrenal gland is found close to the left side of the abdominal aorta and caudal to the origin of the cranial mesenteric artery. The gland measures 6–8 mm, is oval-shaped and usually of a pinkish color. It may also have a grooved surface due to the adrenolumbar vein, which crosses it to enter the vena cava.

The right adrenal gland is more elongated (approximately 8–11 mm long) and is in a more dangerous position in relation to possible surgery. It lies more rostral than the left gland, being close to the point of origin of the cranial mesenteric artery. It should be noted that the right adrenal gland is always related ventrally to the caudal vena cava, which may overlap the medial half of the gland or overlie it completely. The right adrenal gland may also be grooved by the right adrenolumbar vein.

The adrenal glands have been well documented by Holmes (Holmes 1961). Their anatomical placing makes a complete adrenalectomy operation difficult. Their blood supply is basically via vessels from the renal artery and vein and cranial mesenteric artery, though Holmes found variations. In structure, the adrenal cortex has three main zones, as seen in other animals: the glomerulosa, fasciculata, and reticularis plus the zona intermedia and zona juxtamedullaris (Holmes 1961).

Holmes has given an idea of adrenal gland and ovary size in relation to jill body mass. Ferrets in late proestrus or full estrus show an adrenal mass increase (Table 12.2).

Hormonal disorder of the adrenal gland, which is not associated with the pituitary gland, is the overproduction of various sex hormones leading to unilateral or bilateral hyperplasia, adenomas or adenocarcinoma. It is theorized that in the embryonic stage, the ovaries and adrenal glands develop in the same embryonic region and, possibly, some ovarian cells are taken up by the adrenal gland and become part of the outer cortex (Rosenthal 1997). Some stimulation leads to excess sex hormones (especially estradiol) being released and affecting the ferret physiology, male or female (Table 12.3).

The primary clinical sign of AGN is alopecia, gradually affecting the whole body. It is at epidemic levels in pet ferrets in the USA, with incidences rising from 30% in 1993 to 70% in 2003. Approximately 80–90% of cases are unilateral (Finkler 2002). The average age of American ferrets when affected is 3½–4½ years but it has been seen in ferrets from 8 months to 9 years. Additional signs include lethargy and muscle atrophy, pruritus in the jill with vulval swelling, vaginitis, and stump pyometra. In hobs the prostate is affected, showing enlargement and stranguria. Diagnosis is usually on clinical signs and history.

The history (etiology) of affected American pet ferrets is interesting. Basically, they are sterilized at 6 weeks of age, kept in apartments or houses under unnatural lighting and for extended photoperiods. This contrasts to Australian ferrets,

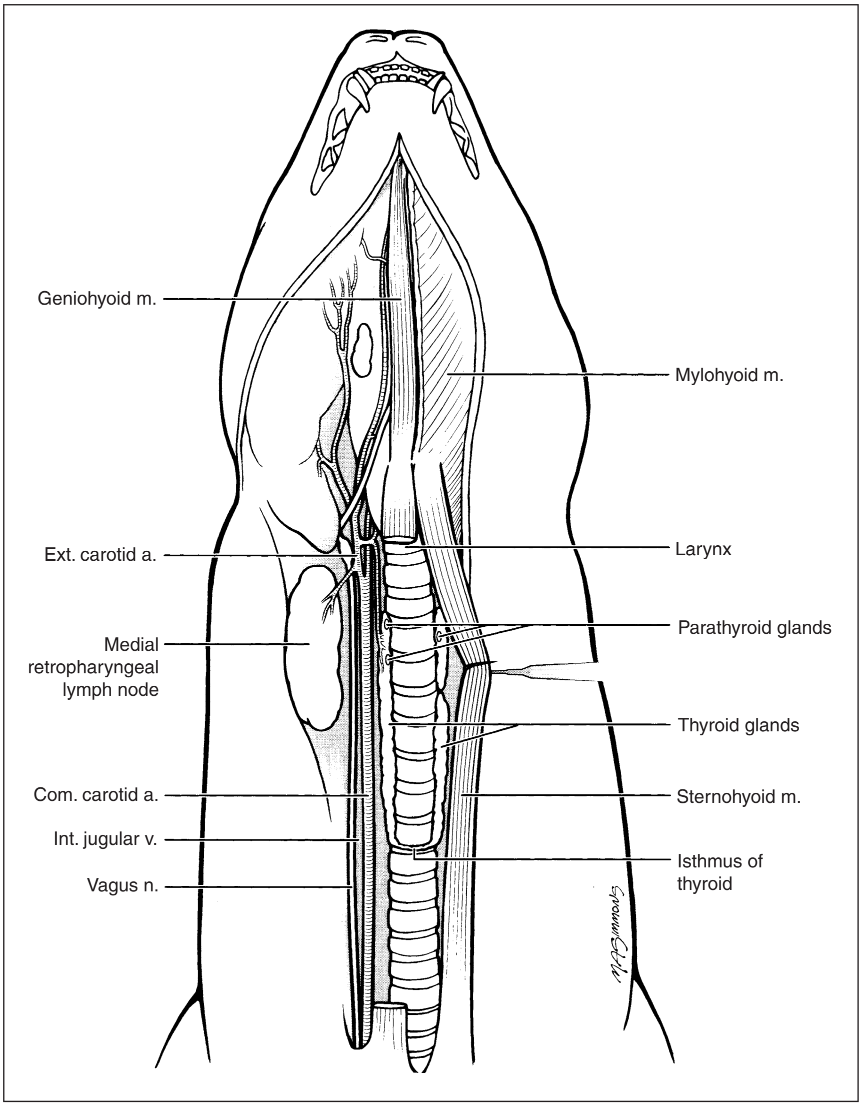

Geniohyoid m.
Mylohyoid m.
Ext. carotid a.
Larynx
Medial retropharyngeal lymph node
Parathyroid glands
Thyroid glands
Com. carotid a.
Sternohyoid m.
Int. jugular v.
Isthmus of thyroid
Vagus n.

Figure 12.24 • Ferret endocrine glands. (Courtesy of Howard Evans.)

which are sterilized at 5–6 months of age and kept outside in cages or in an enclosed "ferret-proof" garden or ferretarium arrangement (Lewington 2003a).

In the case of ferrets it is surmised that early sterilization stimulates the growing adrenal glands to produce sexual hormones in an unnatural position in the body, without the normal negative feedback mechanism of estrogens and androgens on the hypothalamus. The proposed scenario is that the hypothalamus continues to secrete gonadotropin-releasing hormone (GnRH). This gives a continuous stimulation for

Table 12.2 Adrenal gland and ovary weights in the ferret

	Left adrenal (*mg*)	**Right adrenal (*mg*)**	**Paired adrenals (*mg*)**	**Paired ovaries (*mg*)**	**Jill body weight (*g*)**
Group 1: 36 anestrus ferrets	51.3	55.5	107.1	67.7	653.0
Group 2: 11 ferrets in anestrus or early proestrus	37.7	41.0	79.1	111.1	741.0
Group 3: 9 ferrets in late proestrus or full estrus	53.0	57.5	111.0	121.0	747.0

Table 12.3 Estrogen precursor values in normal and AGN affected ferrets

Steroid	Normal ferrets	AGN ferrets
Androstenedione (nmol/L)	6.6	67
DHEAS (mol/L)	0.01	0.03
Estradiol (mol/L)	106	167
17-Hydroxyprogesterone (nmol/L)	0.4	3.2

DHEAS, Dehydroepiandrosterone sulfate
After Rosenthal, K. (1997) In E. V. Hillyer & K. E. Quesenberry (eds.), Ferrets, rabbits and rodents: Clinical medicine and surgery. Philadelphia: WB Saunders, with permission.

the pituitary gland to secrete luteinizing hormone (LH) and follicle-stimulating hormone, (FSH), which in turn stimulate the incorporated ovarian cells in the adrenal gland cortex.

American veterinarians agree that the unnatural photoperiods (living under artificial light) combined with early desexing are predisposing pet ferrets to the disorder. Ferrets are highly sensitive to the photoperiod; unspayed jills are sexually controlled by it. Melatonin is the hormone produced in the dark by the pineal gland; it has been implicated in a wide range of physiologic processes, including reproduction (through its effects on gonadotrophins). Melatonin levels normally increase as the photoperiod decreases. In humans melatonin is considered anticancer. The photoperiod of “in house” pet ferrets is largely determined by artificial lighting and rarely mimics the natural period. Thus, not only are these ferrets subject to abnormally long (or short) photoperiods but there is often a lack of normal seasonal fluctuation. The abnormal melatonin secretion could therefore affect the adrenal gland. Possibly melatonin could be given orally to pet ferrets to prevent the disease but it has only a short action and there is no injectable form as yet (Finkler 2002).

Treatment is either surgical or long-term medication with drugs, many of them human ones and expensive. Surgery for a unilateral AGN case in my own pet ferret has been described (Lewington 2003e) while Bennett describes surgery for a complex bilateral AGN case (Bennett & Pye 2000). Medication without surgery has been described (Finkler 2002; Lewington 2003e) and work on the disease is ongoing in the USA. Actually, AGN cases will live for over a year post-diagnosis without treatment, until complications occur.

The pancreas

The organ is ‘v’-shaped, elongate and lobular, being light pink to bright red on surgical examination. It consists of right and left limbs (lobes) associated with the central mass adjacent to the pylorus (Fig. 12.25). The left limb, shorter than the right, runs along the visceral surface of the stomach with the spleen lateral. It is bi-angular in cross-section and enclosed in the mesoduodenum. Dorsally, it is near the portal vein, left kidney, and left adrenal gland. The right limb (see Fig. 12.15a) follows the descending part of the duodenum on the dorsomedial aspect.

Whereas AGN can be cured, to some extent, insulinoma, a condition of the pancreas, is not and is another ongoing medical problem for mostly American pet ferrets (Fig. 12.26). Raised nodules of pancreatic islet cells over the surface of the organ indicate insulinoma in the ferret.

Insulinoma is primarily found in American pet ferrets where small tumors of the pancreatic islet cells produce a high level of insulin, which can be fatal in producing hypoglycemia due to blood-sugar depression. Thus the normal feedback mechanism, to stabilize the animal with low blood sugar, is compromised by the neoplastic cells. Interestingly, in early cases there is some stimulation of liver gluconeogenesis and glycogenolysis, but the process becomes inefficient. Blood-sugar depletion affects brain function, with deprivation of energy source and resulting dullness and confusion (Quesenberry 1997). Clinical signs of the condition are hind leg weakness and a tendency for the ferret to stare blankly into space and drool excessively. Hypoglycemia leads to seizures and death.

The feeding of ferrets on high carbohydrate, high fiber (processed) foods, as distinct from a natural diet, are thought to be an etiological cause. Ad libitum feeding of in-house ferrets with dry foods will add to the problem. Ferrets should have a high protein, high fat (for energy), low carbohydrate and low fiber diet, and be fed no more than twice daily. General ideas on feeding ferrets have been described (Lewington 2003b).

Treatment of insulinoma is by surgery (Bennett & Pye 2000) and requires special postoperative care (Lewington 2003f). Affected treated ferrets can live for 1–3 years but require owner patience and attention. In AGN and insulinoma prevention is better than cure.

KEY NOTES

- Early neutering and lack of a natural photoperiod may predispose a ferret to adrenal gland neoplasia (AGN).
- The left adrenal gland is more accessible for surgery than the right because the right adrenal is intimately associated with the caudal vena cava.
- The pancreas is commonly a site of insulinoma.

NERVOUS SYSTEM

The ferret brain is about 36 mm long by 24 mm wide and has a normal mammalian structure (Lawes & Andrews 1998). The special senses: hearing, sight, and smell are of interest in relation to conditions and diseases. The visual and auditory systems mature after birth so that kittens open their eyes at 4–5 weeks and can hear at 32 days.

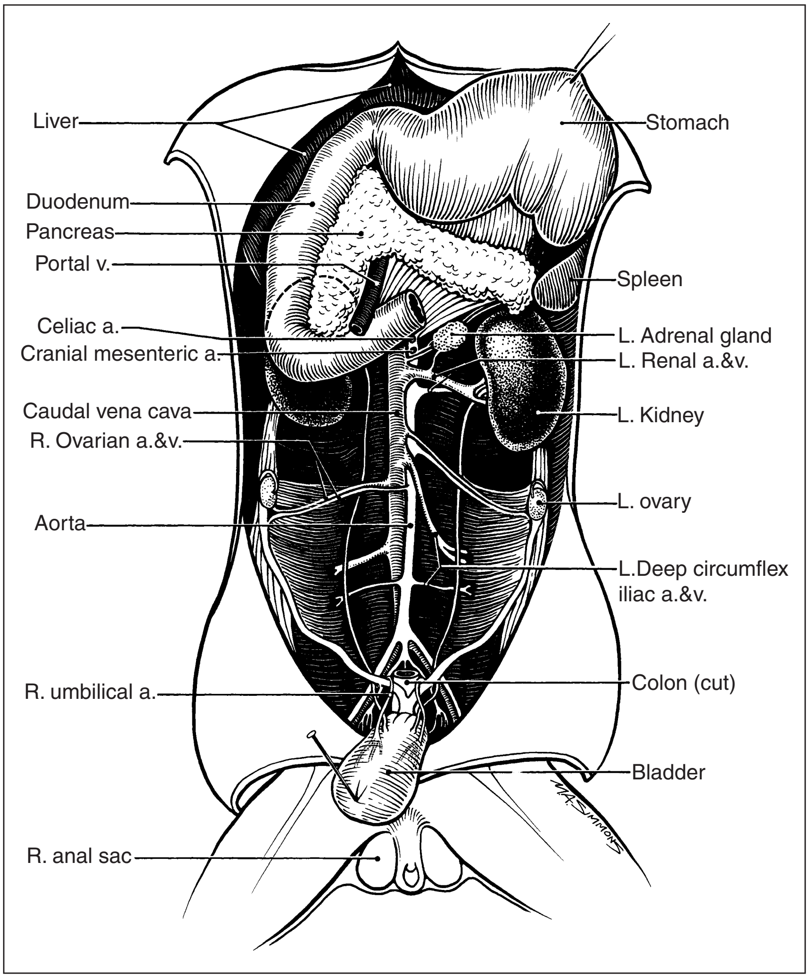

Liver
Duodenum
Pancreas
Portal v.
Celiac a.
Cranial mesenteric a.
Caudal vena cava
R. Ovarian a.&v.
Aorta
R. umbilical a.
R. anal sac
Stomach
Spleen
L. Adrenal gland
L. Renal a.&v.
L. Kidney
L. ovary
L.Deep circumflex iliac a.&v.
Colon (cut)
Bladder
SIMMONS

Figure 12.25 • The ferret pancreas, spleen, and ovaries. (Courtesy of Howard Evans.)

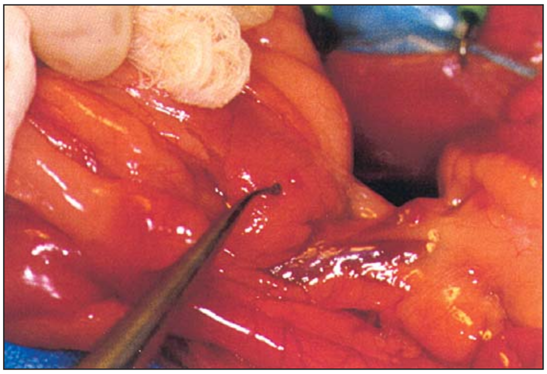


Figure 12.26 • Insulinoma in a ferret. The ring tip microforceps are pointing at a 2 mm nodule typical of insulinoma. Slide courtesy of Prof. Avery Bennett.

Senses

Hearing

The ferret auditory system is physiologically similar to that of the cat, but it is thought auditory response in the ferret is more primitive. Adult ferrets usually respond to sounds in the 4–15 kHz range, while 32-day-old kittens respond to 1–6 kHz but at a higher threshold (Whary & Andrews 1998). Adult frequency response patterns have been recorded at 39 and 42 days. Interestingly, neonates put out distress cries of 100 kHz. The jills with litters respond to all calls above 16 kHz, but this phenomenon is not seen with non-lactating jills presented with neonates.

The question of deafness in ferrets can be a worry but usually, being hunters, ferrets have acute hearing and a keen sense of smell while their sight is more adapted to their nocturnal habit. A Western Australian black-eyed white ferret jill which repeatedly ignored a crying kitten has been recorded as deaf by Amy Flemming (personal communication 1999). It had the Waardenburg syndrome, a dominant genetic fault. Hearing can be checked in ferret kittens at 32 days by their response to a loud clap.

Anatomy of the ear

The external ear consists of a pinna and an external ear canal, which differs markedly in shape from that in the dog and cat (Lewington 1990) (Fig. 12.27). The ferret pinna is set close to the head and half-moon shaped, some 2 cm wide in adult hobs and pointing forward, as is compatible with a

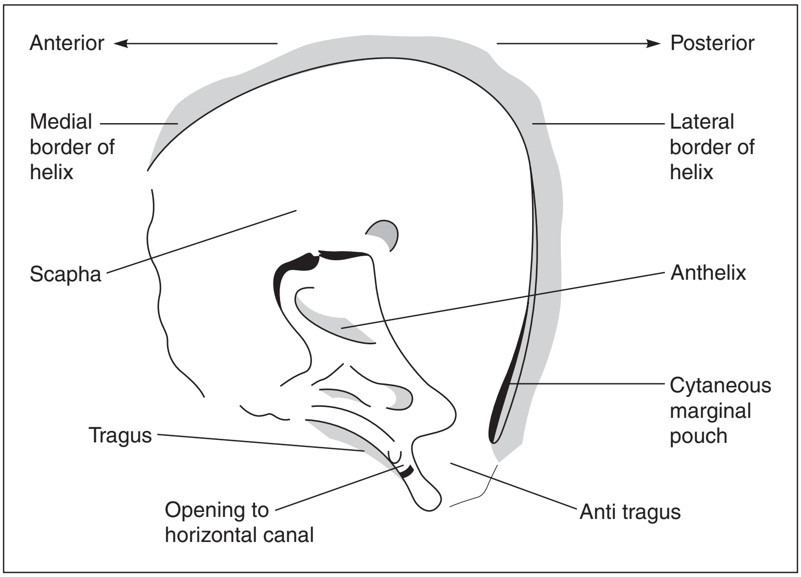

Anterior
Posterior
Medial border of helix
Lateral border of helix
Scapha
Anthelix
Cytaneous marginal pouch
Tragus
Opening to horizontal canal
Anti tragus

Figure 12.27 • Ferret external ear. (By Debbie Squance.)

hunting animal. Some ferrets have a flatter, wider pinna, large compared to the head size, which is possibly a genetic fault.

There is no distinct tubular ear canal as in the dog and cat. The whole ear canal is protected by a screen of fine hairs around the anterior margin. Interestingly, the lateral margin of the ear canal has a more pronounced recession, intertragic incisure-like, which is more tube-shaped than seen in the cat and some 5 mm long. It gives the impression of a miniature aural resection. Almost opposite, medial to the base of the intertragic incisure, is the opening of the horizontal canal, which passes anteriomedially to the tympanic membrane. There is hardly any depth to it. Whether the shape of the ferret external ear makes it prone to otitis has not been shown.

The middle and inner ear is comparable to that of the dog in general structure (Figs 12.28 and 12.29).

The ear pinna can be the site of fight wounds and advanced cases of *Sarcoptes scabies* var. *canis*, which spread from the feet in ferrets. The external ear can be infected with *Otodectes cynotis*, as in dogs and cats. The inner ear may show idiopathic otitis internal (IOI) with head tilting, and loss of balance due to extensive middle ear infections or blood-borne pathogens (Lewington 2003d).

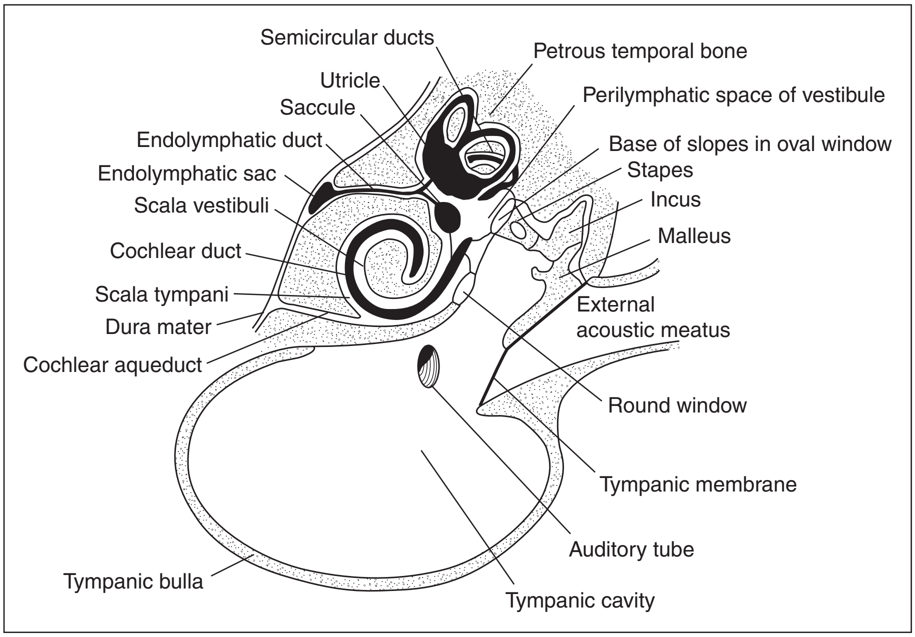

Semicircular ducts
Petrous temporal bone
Utricle
Saccule
Perilymphatic space of vestibule
Endolymphatic duct
Base of slopes in oval window
Endolymphatic sac
Stapes
Scala vestibuli
Incus
Malleus
Cochlear duct
Scala tympani
External acoustic meatus
Dura mater
Cochlear aqueduct
Round window
Tympanic membrane
Auditory tube
Tympanic bulla
Tympanic cavity

Figure 12.28 • Diagram of the structure of the middle and inner ear of the dog. From Getty, R., Foust, H. L., & Presley et al. (1956) Macroscopic anatomy of the ear of the dog. *American Journal of Veterinary Research 17*, 364–375, with permission.

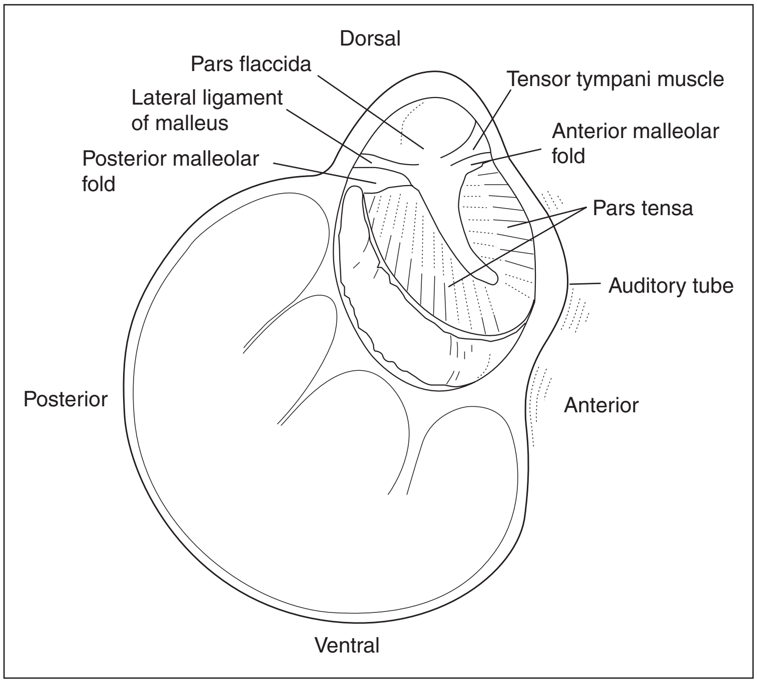


Figure 12.29 • Diagram of the medial face of the lateral wall of the left tympanic cavity of the dog. From Spreull, J. S. A. (1976) Otitis media in the dog. In R. W. Kirk (ed.), *Current Veterinary Therapy V*. Philadelphia: WB Saunders, with permission.

Vision

The ferret's eyesight is poor in comparison to its senses of smell and hearing; it is adapted to nocturnal life, like its polecat ancestor (Lavers & Clapperton 1990). Studies of the ferret visual system have been orientated to such problems as the influence of photoperiods on reproduction, albinism, and its effects on ocular development, and various studies on the ferret neuro-opthalmic development and basic investigation relevant to human eye problem research (Miller 1997). The visual systems are studied utilizing the very immature state of neonate ferret visual systems (Jackson & Hickley 1995).

Clinical examination of the ferret eye involves normal cat and dog tests except for the Schirmer tear test. The eye can be examined using a magnifying loupe and, for internal eye examination, an opthalmoscope in a dark room. Indirect ophthalmology plus a 30 or 40 diopter (D) condensing lens can be used. Eye specialists use a slit lamp biomicroscope.

Comparative studies of sight in mustelids suggest that the short pointed face of a weasel allows both binocular vision forward and a wide arc of monocular vision on each side (King 1989). One author suggests ferrets have mostly monocular but very little binocular vision (Kircher 1997). Another is of the opinion that from their facial conformation there is no difference in range of vision between weasels, stoats, and ferrets (King 1989).

The eye that sees well in dim light achieves this ability at the expense of acuity in bright light (King 1989). Thus, most carnivores see movements rather than pictures but they can be sharp-eyed on focusing in on prey. So, waving a finger in front of a ferret in daytime can be dangerous: the ferret sees and responds to moving objects at speeds of 25–45 cm/s; for example, a mouse in a hurry! (Miller 1997).

The ferret's ability to see objects clearly depends on the optical properties of the eye, which involves retinal sensitivity and optical processing of visual images in the central nervous system. The retinal activity is usually the controlling factor. Optical abnormalities can occur in the ferret eye and the optical quality of this special sense organ is considered moderate. In detail the ferret appears to be 6.8 D (range 5–8 D) hyperopic or farsighted. Of 12 ferrets in one study 4 revealed astigmatism of 0.5 D or greater. Additional faults can be found in the refraction between the two eyes because of the large spherical lenses. This may show up in dim light when the pupil is dilated (Miller 1997). On the question of perception of form, work has been done on the weasel, which can appreciate different letters in form discrimination tests (Herter 1939) to get a food reward, or not, from differently labelled boxes (King 1989). In the ferret image brightness might be a factor as objects brighter than the background stimulate a more effective pre-catching behavior than darker images (Miller 1997).

Color vision in ferrets is possible. Experiments with weasels and stoats (Gewalt 1959; Herter 1939), which have rods and cones in ratios typical of diurnal animals, have shown that the stoat can see at least red and possibly also yellow, green, and blue. The ferret has not been studied but its retina is similar to the cat's in its density of rods and cones, so there is a suggestion that ferrets can detect color (Miller 1997).

In any case the detection of color is of no real advantage in nocturnal animals.

Anatomy of the eye

The ferret has a well-developed nictitating membrane which can be used for ulcer treatment as a third eyelid flap (Lewington 1994). The cornea is relatively large in relation to the eye structure and the lens is nearly spherical and placed back in the posterior eye chamber (Kern 1989). The pupil is a horizontal elliptical slit, not vertical like the cat, and more efficiently protects the eye from strong sunlight.

Retina

The retina is similar in form and vascular pattern to that found in the dog (Miller 1997). The tapetum is well defined with the 7–10 cell layer having a high zinc and cysteine content; the myelinated optic disk is relatively small (Wen et al. 1985). A study of the tapetum lucidum established that the structure is the same in both pigmented and albino ferrets (Tjalve & Frank 1994). The receptor cells in the retina, cones, and rods, differ in function; the cones perceive bright light and colors and are found in large numbers in diurnal species whereas rods are particularly sensitive to low-intensity light and are numerous in the eyes of nocturnal animals (King 1989). Thus the ferret retina has a high proportion of rods in the photoreceptor layer of the ferret eye. The rods predominate to the cones in the ratio 50–60:1 (Jackson & Hickley 1995).

CLINICAL NOTE

The ferret, like other mustelids, having the combination of a large cornea, spherical lens, and a tapetum lucidum highly receptive to dim light, is well-adapted to nocturnal living. The tapetum gives the "eye-shine" glow to nocturnal animals caught in a torch beam.

Photoperiod

The ferret eye, in association with the visual nervous system linked to the pineal gland, is involved with reproduction and also with endocrine problems, for example, the jill ferret estrous cycle is related to photoperiod length. The cycle will begin with extended photoperiods in spring and can be adapted to increasing or decreasing the number of litters per year. A blind ferret will not start estrus. Increasing photoperiods stimulate the hob to become sexually active. It is theorized that an artificial regimen of extended photoperiods may cause adrenal gland neoplasia in the sterilized ferret due to the failure of melatonin production in the continuously light-stimulated pineal body.

Olfaction

The ferret's sense of smell ranks in importance with its sense of hearing (Lavers & Clapperton 1990). Marking territory and scenting another animal's presence and path is common to many mammals. Mustelids are persistent in following the scent of prey.

Nasal anatomy

The pointed face of the ferret has a tapering nasal organ (see Fig. 12.9). The nasal cavity is formed by the maxilla and nasal bones dorsally and laterally, with the maxillary and palatine bones supplying the cavity floor, similar in shape to the long-nosed dog. The bony nasal aperture is composed of two symmetrical halves (Evans & de Lahunta 1971).

The ethmoid bone complex is located between the brain case and the facial part of the skull. It consists of the ethmoid labyrinth, the cribriform plate, and the median bony plate of the nasal septum. The ethmoid labyrinth is composed of many delicate scrolls, as in the dog, that attach to the cribriform plate and occupy the fundus of the nasal cavity. Bony scrolls, the conchae, project into each nasal fossa and with their mucosa act as baffles to warm and clean inspired air. The nasal cavity is therefore one of the first lines of defense against pathogenic invasions. On the other hand it can supply a vascular environment for pathogens to grow and spread if they overcome the body's defenses. The conchae are divided into a small dorsal and large ventral portion, as in the dog. The olfactory mucosa lining the conchae that house the olfactory nerve cells allow infection to invade the brain via the cribriform plate of the ethmoid complex. The ethmoid plate in the ferret does not completely pass ventrally to the cartilage of the nasal septum to divide the nasal fossa as it does in the dog. Thus it is more difficult to pass a nasal tube in the ferret, but it is not impossible (Lucas 2000) (Fig. 12.30).

Clinically, the nasal cavity is an entry point for viral infections, such as canine distemper and human influenza, and a gateway for infection of the lungs by a variety of organisms leading to pneumonia. The closeness of the cribriform plate to the brain meninges can be an entry to such pathogenic fungi as *Cryptococcus neoformans*, leading to acute meningitis in the ferret (Lewington 1997).

INTEGUMENT

The integument of the ferret contains numerous sebaceous glands, which give the animal its musky smell. This is different from musk (anal) gland odor. There are no skin sweat glands and this makes ferrets vulnerable to heat stress in hot climates.

The blackish-brown coloring of the thick outer coat guard hairs varies in the fitch or sable ferret, and ferrets living outside tend to be darker; the undercoat is white to yellow. Albino ferrets, with unpigmented (pink) eyes, and black-eyed whites (white-coated ferrets with dark pigmented eyes) are two other common colors. The silver mitt ferret has white paws. Sable, silver mitt, black-eyed white (BEW) and albino are basic ferret colors (Figs. 12.31–12.34), while the American Ferret Association recognizes a range of 30 coat color variations, derived from breeding programmes in the USA.

The AFA-approved color variations include:

- Silver – dark gray guard hair and a cream-colored undercoat but little or no mask.
- Black-eyed white – pigmented eyes and white coat.
- Chocolate – dark brown guard hairs rather than the characteristic black of sable ferrets.
- Siamese – guard hairs lighter than the chocolate type and with a light-colored mask.
- Panda – white hair on the head and shoulders but a body of various colors.
- Shetland sable – sable body color but with a white stripe placed vertically on the face from the nose to the top of the head (Brown 1997).

Molting

The ferret coat is subject to seasonal molts. With a summer molt sables lighten somewhat; they then darken with the autumn (fall) molt and thicken in coat. This is especially prevalent in ferrets living outdoors, as is usual in Australia, New Zealand, and the UK, compared to indoor-kept American ferrets.

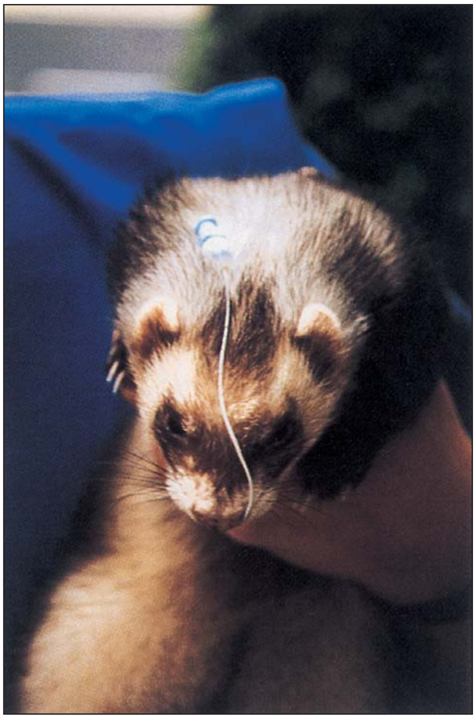


Figure 12.30 • A correctly secured nasogastric catheter. Slide courtesy of Dr. Anthony Lucas.

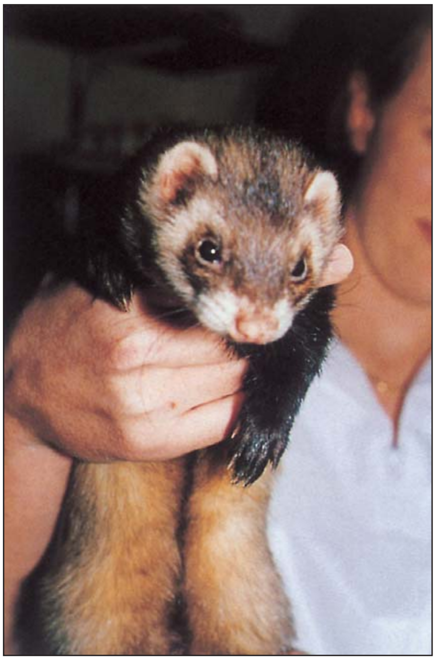


Figure 12.31 • Sable ferret.

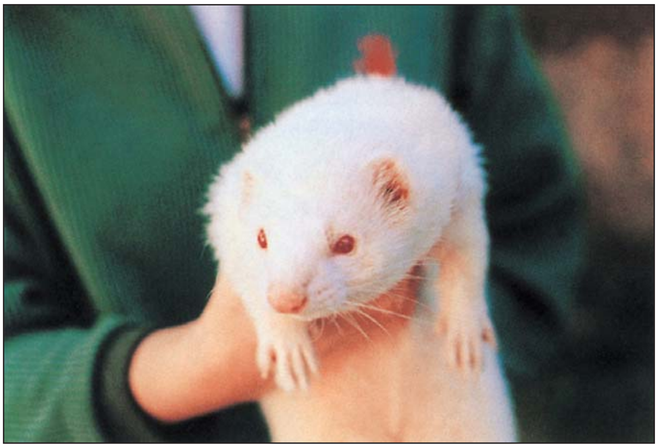


Figure 12.32 • Albino ferret.

KEY POINTS

- The ferret has acute hearing and smell.
- Being nocturnal, rods predominate to the cones in the ratio 50–60:1 (Jackson & Hickley 1995).
- The ferret sees and responds to moving objects better than to stationary objects.
- The visual nervous system and pineal gland are intimately involved with reproduction and subsequent endocrine problems.
- The very narrow ventral space in the nasal conchae makes passing a nasogastric tube difficult.
- Numerous sebaceous skin glands convey the musky ferret smell.
- The lack of sweat glands makes ferrets vulnerable to heat stress.

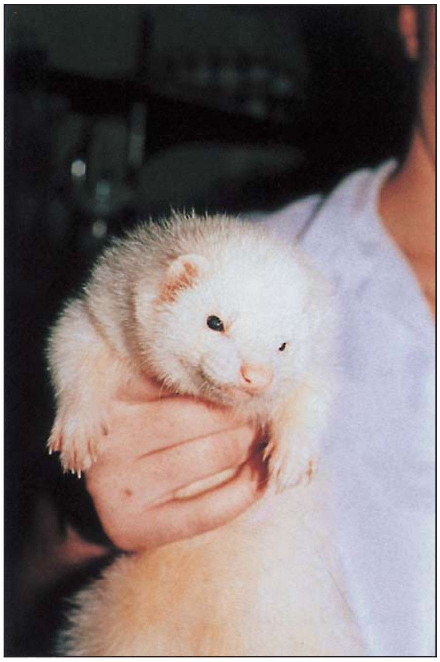


Figure 12.33 • Black-eyed white ferret.

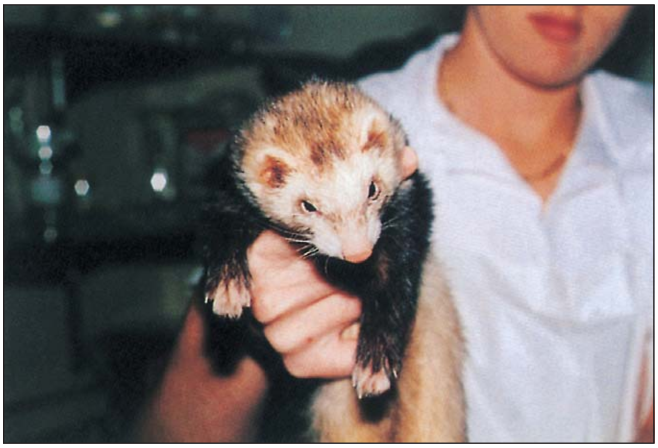


Figure 12.34 • Silver mitt ferret.

REFERENCES

Andrews, P. L. R., Illman, O., & Mellersh, A. (1979) Some observations of anatomical abnormalities and disease states in a population of 350 ferrets (*Mustela furo* L.). *Zeitschrift fuer Versuchstierkunde 21*, 346–353.

Bennett, A., & Pye, G. W. (2000) General surgery. In J. Lewington, *Ferret husbandry, medicine and surgery*. Oxford: Butterworth-Heinemann. pp. 240–250.

Brown, S. (1997) Basic anatomy, physiology, and husbandry. In E. V. Hillyer & K. E. Quesenberry (eds.), *Ferrets, rabbits, and rodent: Clinical medicine and surgery*. Philadelphia: WB Saunders. pp. 3–13.

Curl, J. L., & Curl, J. S. (1985) Restraint device for serial blood sampling of ferrets. *Laboratory Animal Science 35*, 296–297.

Dillberger, J. E. (1985) Polycystic kidneys in a ferret. *Journal of the American Veterinary Medical Association 186*, 74–75.

Esteves, M. I., Marini, R. P., Ryden, E. B., Murphy, J. C., & Fox, J. G. (1994) Estimation of glomerular filtration rate and evaluation of renal function in ferrets. *American Journal of Veterinary Research 55*, 166–172.

Evans, H. E., & An, N. Q. (1998) Anatomy of the ferret. In J. G. Fox (ed.), *Biology and diseases of the ferret*. Philadelphia: Lea and Febiger. pp. 14–64.

Evans, H., & de Lahunta, A. (1971) *Miller's guide to the dissection of the dog*. Philadelphia: WB Saunders. pp. 210–224.

Finkler, M. (2002) *Practical ferret medicine and surgery*. Roanoke, Va.: Roanoke Animal Hospital.

Fox, J. G. (ed.) (1998) *Biology and diseases of the ferret*. Baltimore: Williams and Wilkins. Normal clinical and biologic parameters; pp. 183–210.

Fox, J. G., Pearson, R. C., & Bell, J. A. (1998) Diseases of the genitourinary system. In J. G. Fox (ed.), *Biology and diseases of the ferret*. Baltimore: Williams and Wilkins. pp. 247–272.

Hillyer, E. V. (1997) Urinogenital diseases. In E. V. Hillyer and K. E. Quesenberry (eds.), *Ferrets, rabbits, and rodents: Clinical medicine and surgery*. Philadelphia: WB Saunders. pp. 44–52.

Holmes, R. L. (1961) The adrenal glands of the ferret *Mustela putorius*. *Journal of Anatomy 95*, 325–336.

Jackson, C. J., & Hickley, T. L. (1995) Use of ferrets in studies of the visual system. *Laboratory Animal Science 35*, 211–215.

Jenkins, J., & Brown, S. A. (1993) *A practitioner's guide to rabbits and ferrets*. Lakewood, Co: American Animal Hospital Association. pp. 49–98.

Johnson-Delaney, C. A., & Nelson, W. B. (1992) A rapid procedure for filling fractured canine teeth of ferrets. *Journal of Exotic Animal Medicine 1*, 100–101.

Kern, T. J. (1989) Ocular disorders of rabbits, rodents and ferrets. In R. Kirk (ed.), *Current Veterinary Therapy 10*. Philadelphia: WB Saunders. pp. 681–685.

King, C. (1989) *The natural history of weasels and stoats*. London: Christopher Helm.

Kircher, S. E. (1997) Ophthalmologic diseases in small mammals. In E. V. Hillyer & K. E. Quesenberry (eds.), *Ferrets, rabbits, and rodents, clinical medicine and surgery.* Philadelphia: WB Saunders. pp. 344–345.

Lavers, R. B., & Clapperton, B. K. (1990) Ferret. In C. M. King (ed.), *The handbook of New Zealand mammals*. Oxford: Oxford University Press. pp. 320–330.

Lawes, I. N., & Andrews, P. L. R. (1998) Neuroanatomy of the Ferret brain. In J. G. Fox, *Biology and diseases of the ferret*, 2nd edn. Baltimore: Williams and Wilkins. pp. 71–102.

Lewington, J. H. (1990) Examination of ferret ear. *Control and Therapy 152*, 195–196. Sydney, NSW: Post-Graduate Foundation, University of Sydney.

Lewington, J. H. (1994) Third eyelid flap for treating corneal ulcer in the ferret. *Control and Therapy 179*, 675. Sydney, N.S.W.: Post-Graduate Foundation, University of Sydney.

Lewington, J. H. (1997) Cryptococcosis in the ferret. *Control and Therapy 195*, 923–924. Sydney, NSW: Post-Graduate Foundation, University of Sydney.

Lewington, J. H. (2003a) *Ferret husbandry, medicine and surgery*. Oxford: Butterworth-Heinemann. Accommodation; pp. 27–53.

Lewington, J. H. (2003b) *Ferret husbandry, medicine and surgery*. Oxford: Butterworth-Heinemann. Nutrition; pp. 54–74.

Lewington, J. H. (2003c) *Ferret husbandry, medicine and surgery*. Oxford: Butterworth-Heinemann. Diseases of internal organs; pp. 153–176.

Lewington, J. H. (2003d) *Ferret husbandry, medicine and surgery*. Oxford: Butterworth-Heinemann. Diseases of the ferret ear, eye and nose; pp. 177–198.

Lewington, J. H. (2003e) *Ferret husbandry, medicine and surgery*. Oxford: Butterworth-Heinemann. Endocrine diseases; pp. 211–215.

Lewington, J. H. (2003f) *Ferret husbandry, medicine and surgery*. Oxford: Butterworth-Heinemann. Insulinoma; pp. 218–219.

Lewington, J. H. (2003g) *Ferret husbandry, medicine and surgery*. Oxford: Butterworth-Heinemann. Ferret Vasectomy and Orthopaedic Surgery; pp. 251–260.

Lucas, A. (2000) Ferret emergency techniques. In J. Lewington, *Ferret husbandry, medicine and surgery*. Oxford: Butterworth-Heinemann. pp. 261–271.

Manning, D., & Bell, J. A. (1990) Lack of detectable blood groups in domestic ferrets: Implication for transfusion. *Journal of the American Veterinary Medical Association 197*, 84–86.

Miller, P. E. (1997) Ferret ophthalmology. *Seminar on Avian and Exotic Pet Medicine 6*, 146–151.

Miller, P. E., & Pickett, J. P. (1989) Zygomatic salivary gland mucocoele in a ferret. *Journal of the American Veterinary Medical Association 194*, 1437.

Owen, C. (1984) Ferret. In I. L. Mason (ed.), *Evolution of Domesticated Animals*. London: Longman. pp. 225–228.

Pass, D., Butler, R., Lewington, J., & Thomas, J. (1993) *Veterinary care of birds, rodents, rabbits, ferrets and guinea pigs*. Perth, W.A.: Murdoch University, Foundation for Continuous Education.

Pitt, F. (1921) Notes on the genetic behaviour of certain characters in the polecat, ferret, and in polecat-ferret hybrids. *Journal of Genetics 11*, 100–115.

Quesenberry, K. E. (1997) Insulinoma. In E. V. Hillyer & K. E. Quesenberry (eds.), *Ferrets, rabbits, and rodent: Clinical medicine and surgery*. Philadelphia: WB Saunders. pp. 85–90.

Rosenthal, K. (1994) Ferrets. *The Veterinary Clinics of North America Small Animal Practice 24*, 1–23.

Rosenthal, K. L. (1997) Adrenal gland disease. In E. V. Hillyer & K. E. Quesenberry (eds.), *Ferrets, rabbits, and rodents, clinical medicine and surgery*. Philadelphia: WB Saunders. pp. 91–98.

Smith, G. (1982) Cranial morphology and ontogeny in the ferret. Self-published.

Tjalve, H., & Frank, A. (1994) Tapetum lucidum in the pigmented and albino ferret. *Experimental Eye Research 38*, 341–351.

Wen, G. Y., Sturman, J. A., & Shek, J. W. (1985) A comparative study of the tapetum, retina and skull of the ferret, dog, and cat. *Laboratory Animal Science 35*, 200–210.

Whary, M. T., & Andrews, P. L. R. (1998) Physiology of the ferret. In J. G. Fox, *Biology and diseases of the ferret*, 2nd edn. Baltimore: Williams and Wilkins. pp. 103–148.

Willis, L. S., & Barrow, M. V. (1971) The ferret (*Mustela putorius furo*) as a laboratory animal. *Laboratory Animal Science 21*, 712–716.

Index

Clinical notes follow the *anatomy/physiology* of the named animals or groups.
for specific information and illustrations *see* species names; for general information *see* group names (e.g. amphibians).

A

adrenal gland neoplasia (AGN), ferret 248, 249, 250-2
adrenal glands rate 221
  bird 145
  rat 221
  lizard 71
  rabbit 190
  reptile 34-5
Agalychnis callidras (Red-eyed tree frog) 5, 8
Agama agama (Rainbow lizard) 32
Agamidae (lizards) 58-9
Amblyrhynchus cristatus (Galapagos marine iguana) 30, 58
Ambystoma mexicanum (Mexican axolotl) 3, 6, 11
Ambystoma tigrinum (Tiger salamander) 11
amniotic egg 18, 34, 140-3
amphibian anatomy/physiology
  cardiovascular system 8
  dentition 10
  digestive system 9-10
  endocrine system 11
  hematolymphopoiesis 8-9
  hydrational homeostasis 7
  immune system 8-9
  integument 12-13
  metabolism 5-7
  nervous system 11-12
  reproductive system 10-11
  respiratory system 9
  senses/sensory organs 12
  skeletal system 7
  taxonomy 3-4, **5**, **6**
  thermoregulatory homeostasis 5-6
  tongue 10
  urinary system 10
amphibian clinical notes
  administration of medications 8
  epithelial uptake of toxins/treatments 13
  handling 13
  intubation 9
  venepuncture sites 8, 9, 13
Amphisbaenai spp. (Worm lizards) 57-8
Amphiuma spp. (Mud eels) 7
anapsid skull 24
Anguis fragilis (Slowworm) 34, 57
anisodactyly 112
Anseriformes, characteristics **97**, **157-8**
Anura 3, **5**
Ara ararauna (Blue and gold macaw) 102
Archaeopteryx 98
aspergillosis 126
atropine, atropinesterase 171
autotomy, lizards 63-4
azurophils 25

B

Basilicus spp. 58, 62
bird anatomy/physiology 97-161
  see also bird clinical notes; bird taxonomy; Psittaciformes; waterfowl
  adaptation to arid environment 138
  adrenal glands 145
  air sacs 121-5
    abdominal 125
    caudal/cranial thoracic 125
    cervical 124
    clavicular 124
  appendicular skeleton 105-6
  arterial system 113-15
  axial skeleton 103-5
  beak 126-8, 149
  blood components 116-17
    eosophils 117
    erythrocytes 116-17
    heterophils 117
    lymphocytes 117
    monocytes 117
    thrombocytes 117
  blood loss 117
  breathing muscles 125
  breathing/gas exchange 124-5
  bronchi 121-2
  brood patch 151
  bursa of Fabricius 118, 135
  cardiovascular system 113-17
  carina 104
  carnivorous birds 132
  casting (intestinal reflux) 134
  caudal vertebrae 104
  cecum 135
  celomic cavities 112-13
  ceres 128, 139
  cervical vertebrae 103-4
bird anatomy/physiology—*cont'd*
  chicks 143-4
  clavicle and coracoid 105
  cloaca 135-6
  coprodeum 135-6
  cranial kinesis 101
  crop (ingluvies) 130-1
  crop milk 131
  digestive system 125-36
  diving birds, cardiac physiology 116
  drinking 130
  ear, external/middle/inner ear 148
  eggs 143
  endocrine system 142, 144-5
  esophagus 130-1
  external adnexa 146
  eyelids 146
  eyes 146-8
  feathers 151-6
    bristles 154-5
    care 150
    color 154-8
    contour 152-3, 155
    development 153
    down 154-5
    filoplumes 154-5
    follicles 151-2
    hyopenna 154-5
    remiges and rectrices 152
    semiplumes 154-5
    structure 151-3
    tail 153
    wing 152-3
  feeding 130
  femur 110-11
  flight 106-7, 152-3
    altitude 117
    feathers 152-3
    skeletal modifications 100
  gaseous exchange 124-5
    cross-current vs one-way air flow flow 124
  gastrointestinal endocrine cells 145
  'glycogen body' 145
  gout 138
  granivorous birds 132
  heart physiology 116
  hormones 142, 143-5
  humerus 106
  immune system 118
  infraorbital sinus 119
  integument 149-51

bird anatomy/physiology—*cont'd*
  intestinal reflux 134
  isthmus (intermediate digestive zone) 133
  kidneys 136-7
    cortical nephrons 136
    medullary nephrons 137
    nephrons 136-7
  large intestines
    ceca 135
    cecotrophy 135
  large/small intestines 135
  larynx 119,120
  liver 134
  longevity 97
  lung rigidity 124
  lungs 121-4
  lymphatic system 118
  mandible 102-3
  manus, radius and ulna 106-7
  metabolism 97-9
  molting 158
  nasal cavity 118-9
  nasal conchae 119
  nasal/salt gland 119, 137
  nervous system 145-9
  orbital glands 146
  oropharynx 129-30
  osmoregulation 137
  ossification of bones 100
  pancreas 135, 145
  parabronchi 122
  parathyroid glands 145
  patagia 151
  pectoral girdle 105
  pectoral muscles 109
  pelvic girdle 105-6
  pelvic limbs 110-12
    anisodactyly/zygodactyly/palmate 112-13
  pericardial cavities 113
  peritoneal cavities 113
  phalanges 112
  pineal gland 138-9, 144
  pituitary gland 143-4
  pleural cavities 113
  podotheca 150-1
  premaxilla 100-2
  proctodeum 136
  propatagium 109-10
  proventriculus 132-3
  pylorus 134
  regurgitation 130
  renal blood supply 137
  renal portal system 115
  reproductive system, female 140-3
    egg formation 140-3
    endocrine control 142
    infundibulum 141
    isthmus 141
    magnum 141
    ovary 141
    oviduct 141
    oviposition 142-3
    ovulation 142
    post egg laying 143
    uterus 141
    vagina 142-3
  reproductive system, male 139-40
    phallus 140
    testes 139-40
  respiration rate 125
  respiratory system 118-25
    air sacs 124-5
    breathing/gas exchange 124-5
  rete mirabile 114

bird anatomy/physiology—*cont'd*
  salivary glands 129-30
  scapula 105
  senses/sensory organs 146-9
    hearing 148
    olfaction 148-9
    sight 146-8
  sex determination 139
  sexual maturity 141
  size 97
  skeletal system 100-13
  skull 100-3
  spleen 118
  sternum 104-5
  stomach 132-4
  synsacrum 104
  syrinx 120-1
  tail 153
  tarsometatarsus 111
  thermoregulation 99
  thoracic vertebrae 104
  thymus 118
  thyroid gland 144
  tibiotarsus 111
  tongue 129-30
  trachea 120
  ultimobranchial bodies 145
  ureter 137
  uric acid/urine 137-8
  urinary system 136-8
  urodeum 136
  uropygial gland 150
  venous system 115-16
  vent 136
  ventriculus (gizzard) 133-4
  wing feathers 152-3
  wing musculature 107-9
  wing pinioning 107
  wings 105-7, **108**
  see also wings
bird clinical notes
  aspergillosis 126
  asphyxiation 125
  atherosclerosis 116
  blood smears 117
  bone splintering 100
  brachiocephalic trunks 114
  bursa of Fabricius 118, 135
  calcium deposition in egg 138
  castration, surgical 140
  ceres in budgies 128, 139
  crop impaction 130
  crop lavage 129
  crop sampling 131
  dehydration and gout 138
  duodenum 135
  egg peritonitis 113
  'egg-binding' 142-3
  emaciation signs 98
  fasting and hypoglycemia 126
  fungal granulomas 14, 121
  goiter 144
  hepatic disease 134
  humerus fractures and air sac infections 124
  intramuscular injection site 109
  intraosseus catheter placement 107
  iodine deficiency 144
  iron storage disease 134
  lameness and renal tumors 136
  lymph glands 118
  mydriatics 147
  nares 119
  nasal(salt) glands 137

bird clinical notes—*cont'd*
  night vision 148
  nutritional osteodystrophies 112
  ovariectomy 141
  ovary retention 140
  parabronchial appearance 122
  prepping of surgical sites 99
  propatagial tears 110
  rehydration 119
  skin propertes 149
  syrinx, in drakes 121
  tarsometatarsus malformation 111
  venepuncture sites 115-16
  ventilation care 122, 125
  wing drop: coracoid fracture 106
bird taxonomy, orders **97**, **157-8**
bird's nest soup 130
black rat 209
blood shunting
  birds 99
  reptiles 20, 24-5
blood urea nitrogen (BUN) 244
Boidae 77-8
bone structure
  birds 100
  reptiles 21
brachiocephalic trunks 114
brown fat 167, 189
brown rat *see also* rat
Bubo bubo (Eagle owl) 111
Bufo marinus (Giant toad) 13

C

Cacatua sulphurea (Sulphur-crested cockatoo) 108
caecilians (Gymnophiona) 4, **6**, 7
calcium deposition, bird's egg 138
calcium/phosphorus, nutritional osteodystrophies 22, 112
calculi
  ferret 248
  rabbit 189
caloric needs, amphibians **6**
Carnivora, taxonomy 165-6
Caudata 3, **6**, 7
Caviomorpha (Hystricomorpha) 166, 197-208
  see also guinea pigs
cecotrophy
  birds 135
  guinea pigs 201,203
  hamsters 229
  rabbits 163, 185-7
Chamaeleo calyptratus (Yemen veiled chameleon) 59-60
Chameleonidae 59
Chelonia
  Cryptodira 41, **43**
  Pleurodira 41, **43**
  taxonomy and classification 18, 41, **43**
  see also tortoises and turtles
chitin, digestion 28
chromodacryorrhea 223
Colubridae 77-8
Columbiformes, characteristics **97**, **157-8**
columella 35
coprophagy *see* cecotrophy
creatinine, blood urea nitrogen (BUN) 246
Cricetidae 227-36
Cricetulus griseus (Chinese hamster) 235

Crocodylia
  taxonomy and classification **18**
  thecodont dentition 27-8
Crotalus spp. (Rattlesnakes) 88, 92
Cryptodira 41
Cygnus olor (Mute swan) 97, 104

D

dacryocystitis 190
Dendrobates spp. (Arrow poison frogs) 13
D. tinctorius (Dyeing poison frog) 4-5, 10, 13
dentition
  acrodont, lizards 27-8, 66-7
  amphibians 10
  ferret 241-44
  guinea pig 201
  hamster 227
  mammals 167-8
  pleurodont, lizards/snakes 27-8, 67, 87
  polyphyodonty 27
  rabbits 177-8
    incisor malocclusion 177, 180
  rat 214-15
  rodents 167-8
  snake 87
  thecodont, crocodiles 27-8
diapsid skull 24
Dispholidus typus (Boomslang) 78, 88
dog, ear anatomy 254, 255
'drinking patch' (amphibians) 7
dystocia, guinea pig 207, 208

E

ear anatomy
  bird 148
  dog 256, 257
  ferret 254-7
  rat 224
ear ossicles 165
egg peritonitis 113
'egg-binding' 142-3
eggs, amniotic 18, 34, 140-3
Elapidae 77-8
Emys orbicularis (European pond turtle) 49
erythropoiesis, control in birds 117
estivation 21
Eublepharidae 59-60
Eublepharius macularius (Leopard gecko) 32, 36, 60, 70, 73

F

Falconiformes, characteristics **97**, **157-8**
fangs, front- vs rear-fanged snakes 87-8
ferret anatomy/physiology 237-61
  abdominal viscera 242, 246-8
  adrenal glands 252-4
  bladder 248
  blood PCV 240
  blood sampling 239-40, 241
  cardiovascular system 238-40
  coat/color 258-60
  creatinine, blood urea nitrogen (BUN) 246
  dentition 240-44
  digestive system 241-45
  ear anatomy 254-7
  endocrine system 252-4
  estrous cycle 251-2
  eye anatomy 258
  feeding 254
  female reproductive system 250-52
ferret anatomy/physiology—*cont'd*
  gastrointestinal tract 244
  head and neck 243
  hearing 253-7
  heart 238, 237
  integument 258-60
  intestines 244-5
  kidneys 246-8
  liver 245
  lungs 240-1
  male reproductive system 249-50
  masseter muscle 244
  molting 259
  musk glands 245
  nasal anatomy 258
  nervous system 254-8
  olfaction 258, 259
  ovaries 250-1
  pancreas 245, 254
  parathyroid 252
  pharynx 243
  photoperiod 254, 258
  prostate gland 249-50
  reproductive system 248-51
  respiratory system 240-1
  retina 258
  salivary glands 244, 245
  senses/sensory organs 254-8
  skeletal system 237-8
  skull 238, 239, 243
  spleen 245
  testes 249
  thyroid 252
  tongue 244
  ureters 248
  urinary system 246-8
  uterus 251
  vision 257-8
ferret clinical notes
  adrenal gland neoplasia (AGN) 250, 251, 252-4
  alopecia 252
  anesthesia 241
  bite strength 244
  cardiopulmonary resuscitation 241
  castration and vasectomy 249
  cystic calculi 248
  deafness 255
  hyperestrogenism (postestrus anemia) 251
  insulinoma 254, 255
  molar root abscess 244
  ovariohysterectomy 251
  photoperiod 254, 258
  prostatic cysts 250
  temporary teeth, kits 241
  venepuncture sites 239, 241
  vision 258
  Waardenburg syndrome 255
freeze tolerance 6
frogs (Anura) 3-5
fungal granulomas, birds 14, 121
Furcifer pardalis (Panther chameleon) 63-4

G

Galliformes, characteristics **97**, **157-8**
Gekkonidae 59-60
gerbil 225
goiter 144
golden hamster *see* hamster
granulomas, fungal 14, 121
growth, reptiles 22
guanophores 37
guinea pig anatomy/physiology 197-208
  abdominal viscera 204
  appendicular/axial skeleton 198
  blood cell features 199-200
  cardiovascular system 199-200
  cecotrophy 201, 203
  cecum 202
  coat color and variety 207-8
  colon 202-3
  copulatory plugs 207
  dentition 201
  digestive physiology 201
  digestive system 201-203
  drinking 201
  endocrine system 207
  esophagus 202
  estrus 205-6
  external genitalia 197-8, 199
  feeding behavior 201
  female reproductive system 197-8, 205-6
  gestation 207
  hearing 207
  immune system 200
  integument 207-8
  intestines 202
  Kurloff cells 200, 207
  lactation 197, 207
  liver 203
  lymph nodes 200
  lymphocytes 199-200
  male reproductive system 197, 204-5
  mammary glands 197, 206
  metastatic mineralization 201
  olfaction 207
  oral cavity 201
  orbital contents 207
  pancreas 203
  parturition and lactation 207
  perineal glands 208
  pharynx 202
  reproductive system 204-7
  respiratory system 200
  salivary glands 201-2
  sebaceous glands 208
  senses/sensory organs 207
  sexual maturity 206
  sight 207
  skeletal system 198
  skull 198, 202
  spleen 200
  stomach 202
  thermoregulation 197
  thymus 200
  urinary system 203-4
  venepuncture 199
  vibrissae 208
  vitamin C 201
guinea pig clinical notes
  cystic ovaries 206
  cystitis and obstruction in males 205
  dehydration 201
  endotracheal intubation 200
  molar malocclusion 201
  pubic bone widening and dystocia 207, 208
  Streptococcus zooepidemicus abscessation 200
  vitamin supplementation 201
Gymnophiona 4, **6**, 7

H

hamster anatomy/physiology 227-36
  abdominal cavity 228, 231-3
  cardiovascular system 228

hamster anatomy/physiology—*cont'd*
  cheek pouch 230-1
  dentition 229
  digestive system 229-31
  endocrine system 233-4
  estrous cycle 232
  external genitalia 227-8
  feeding patterns 229
  female reproductive system 231-3
  flank glands 234
  gestation 231-3
  hearing 234
  hibernation 227
  integument 234
  intestines 231
  Jacobson's organ 234
  liver 231
  male reproductive system 231
  mammary glands 233
  olfaction 234
  pancreas 231
  photoperiod 227
  reproductive system 231-3
  respiratory system 228-9
  Russian hamster 235
  senses/sensory organs 234
  sight 234
  skeletal system 228, 229, 230
  skull 230
  stomach 231
  taste 234
  thermoregulation 227
  touch 234
  urinary system 230
  venepuncture 228
hamster clinical notes
  testicle size 230
  vaginal pouches 232
Harderian gland
  rabbit 192
  rat 223
  snake 36
heat sensing, sixth sense 91-2
Heloderma horridum (Beaded lizard) 67-8
Heloderma suspectum (Gila monster) 67-8
hematolymphopoiesis, amphibians 8-9
herbivory
  lizards 18, 29, 68-9
  plant digestion 29
hibernation
  aquatic 21
  estivation 21
  fasting in reptiles 29
  hamster 227
  mammals 169
  reproductive synchronization 21
  stages 21
  tortoises and turtles 21, 42
  trigger factors 21
  see also thermoregulation
hydrational homeostasis, amphibians 7

I
Iguana iguana (Green iguana) 23, 33, 58-9, 62-3, 68, 71
Iguanidae 58
insulinoma, ferret 252, 253
intracardiac shunt 25
iodine deficiency 144
iridescence 37
iridophores 6, 37
iron storage disease 134

J
Jacobson's organ 35

K
Kurloff cells 200, 207

L
lacrimal gland 73, 192
Lagomorpha
  taxonomy 166-7
  see also rabbits
Leporidae 173-95
light, and thermoregulation 20
lizard anatomy/physiology 57-75
  autotomy 63-4
  blood squirts 64
  breeding season 70
  cardiovascular system 64
  dentition 66-7
    acrodont 67
    egg tooth 67
    pleurodont 27-8, 67
  digestive system 67-9
  drinking 68
  ecdysis 73
  eyes/lids 73
  female reproductive system 32-3, 68, 71-2
  herbivory 18, 29, 68-9
  integument 73-4
  limbs 61-2
  longevity 57
  lungs 65-7
  male reproductive system 32, 68, 70-1
  oviparity/vivparity 72
  parthenogenesis 72
  pectoral/pelvic girdles 61-2
  prehension of food 67
  reproductive system 70-2
  respiratory system 65-6
  salt glands 69
  senses/sensory organs 72-3
  size 57
  skeletal system 60-4
  skin glands 73-4
  skull 60-1
  tail 62-4
  taxonomy **57-8**
  thermoregulation 58
  tongue 68
  urinary system 69
  venepuncture sites 64
  venom 68
  see also reptiles
lizard clinical notes
  adrenal glands 71
  amputation of hemipenes 71
  autotomy 63
  eyelids/lacrimal glands 73
  habitat requirements 20
  incision sites 64
  intercostal muscles 6
  nephromegaly 69
  neutering 71
  periodontal disease 67
  post-ovulatory retention of ova 72
  sex differentiation 71
  tooth replacement 67
  see also reptile clinical notes
lungs
  multicameral 26, 50, 66
  paucicameral 26, 65
  unicameral 26, 65

M
mammals
  dentition and gnawing 169-70
  general characteristics 165-72
  heart 165
  taxonomy 165-8
  thermoregulation 167, 173
  uterus 164, 251
  see also ferrets; guinea pigs; hamsters; rabbits; rat; rodents
mammary glands 197, 206, 211, 221,233
  tumors, rat 222
masseter muscle 165, 167-8
  ferret 244
  rat 215
melanophores 6, 37
melatonin 253
Mesocricetus auratus (Syrian hamster) 225-36
mud eels 7
Muridae 209-25, 229
Mustela putorius furo see ferret
Mustela putorius putorius (Polecat) 237
Mustelidae 237-61
mydriatics 147
Myomorpha 168

N
nasal glands *see* salt glands
neoteny 3, 11
nutritional osteodystrophies 22, 112

O
osmoregulation, reptiles 29-31
osteodystrophies 22, 112
oviparity 33, 72
oxygen starvation 25

P
Passeriformes, characteristics **97**, **157-8**
patagia 151
Phodopus sungorus (Russian hamster) 235
phosphorus
  and calcium, balance 189
  nutritional osteodystrophies 22, 112
photoperiod
  ferrets 254, 258
  hamster 227
  rat 209, 221
Phrynosoma cornutum (Horned lizard) 64
Phyllobates spp. (Arrow poison frog) 13
Phyllomedusa spp. (South American tree frogs) 7, 10
Physignathus cocincinus (Water dragon) 59, 67
pineal gland 138-9, 144, 193
placental mammals, uterus 164, 251
plant digestion, reptiles 29
Pleurodira 41
pleurodont dentition, lizards, snakes 27-8, 67, 87
pododermatitis 193-4
podotheca 150-1
Pogona vitticeps (Bearded dragon) 58, 61, 67, 72
polecat 237
polyphyodonty 27
preferred optimal temperature zone (POTZ) 6, 19
prolactin 193

propatagium 109-10
  tears 110
proventriculus 132-3
Pseudemys (Trachemys) scripta (Red-eared terrapin) 33, 42, 43, 48, 49, 53
Pseudobranchus spp. 7
Psittaciformes
  aspergillosis 126
  beak malocclusion 149
  blood sampling 116
  ceres in budgies 128, 139
  characteristics **97**, **157-8**
  crop and gizzard 130-4
  feet 112
  general anatomy 131-2
  heart 114
  hepatomegaly 114
  plumage 150
  sex determination 139
  sinus infections 120
  skeleton 102-5
  skull 119
  syrinx 120
  vitamin A deficiency 129
pubic bone widening and dystocia, guinea pig 207, 208
Python molorus
  ingesting food 83
  thermogenesis 19, 34

R
rabbit anatomy/physiology 173-95
  abdominal viscera 182-6
  adrenals 192
  anatomy, external 173-4
  blood cells 177
  calcium metabolism 189
  cardiovascular system 176-7
  cecotrophy 185-6
  cecum 184-5
  circadian rhythms 186
  coat color 193
  colon 186
  dentition 179-81
  digestive system 179-88
  drinking 188
  endocrine system 192-3
  esophagus 182
  external genitalia 174
  eyes 192-3
  feces, hard/soft (cecotrophs) 187
  feeding/diet 179, 186
  feet 193
  female reproductive system 174-5, 190-1
  fusus coli 186
  hair 193
  Harderian gland 192
  head and neck 174
  hindgut 184-6
  immune system 178
  integument 193
  kidneys 188-9
  lacrimal gland 192
  lactation 191
  liver and bile 188
  male reproductive system 174-5, 190
  mandible 180
  mastication 180-1
  milk oil 183
  molting 193
  nasolacrimal duct 192
  neonates 191
    stomach 183
rabbit anatomy/physiology—*Cont'd*
  oral cavity 179-80
  origins 173
  ovulation 191
  pancreas 188
  parturition 191
  phosphorus: calcium balance 189
  pinnae 174
    as injection sites 177
  pregnancy and pseudopregnancy 191
  reproductive system 190-1
  respiratory system 178-9
  salivary glands 182
  scent glands 193
  senses/sensory organs 192
  skeletal system 174
  skull 180-82
  small intestine 183-4
  stomach 183
  taxonomy 165-8
  thermoregulation 167, 173
  third eyelid gland 192
  tongue 181
  urinary system 188-90
  urine 189
  venepuncture sites 177
  vitamin D 190
  water intake 188
  weaning 183
rabbit clinical notes
  calculi 189
  cardiopulmonary resuscitation 179
  care pre/during anesthesia 178, 179, 183
  cecum, care 184-5
  dacryocystitis 192
  dehydration 187
  dewlap, dermatitis 174
  feeding and intestinal stasis 179
  hepatic lipidosis 188
  incisor malocclusion 179, 182
  injection sites 177, 193
  mandibular prognathism 180
  nares, care when touching 178
  nursing kits 191
  phosphorus balance 189
  pododermatitis 194
  polydipsia 188
  spaying 191
  stomach distension 183
  stomach post-mortem 183
  stress, surgery, diet change 186
  trichobezoars 183
  urine 190
  weaning 183
Rana catesbeina (Bullfrog) 10
Rana pipiens (Northern leopard frog) 13
rat anatomy/physiology 209-26
  abdominal cavity 216-17, 219
  adrenal glands 222
  appendicular skeleton 212
  axial skeleton 211
  birth 222
  cardiovascular system 212-13
  clitoral (preputial) glands 221
  dentition 210, 214-5
  digestive system 214-19
  ears 224
  endocrine organs 222-3
  estrous cycle 221-22
external genitalia 210-11, 212
  eyelids 223
  eyes 210
  feet 210
  female reproductive system 210-11, 220-1
  gestation 222
  Harderian gland 223
  head 209-10
  hearing 223-4
  immune system 213
  incisors 214-5, 217
  integument 224
  lacrimal gland 223
  large and small intestine 217
  liver 217
  longevity 209
  male reproductive system 210, 219-20
  mammary glands 211, 221
  masseter muscle 215
  mastication muscles 215, 217
  molars 215
  nasal cavity 213
  olfaction 224
  oral cavity 214
  pancreas 217, 219
  parathyroid 222
  photoperiod 209, 221
  pituitary gland 222
  reproductive physiology 221-222
  reproductive system 219-222
  respiratory system 213
  salivary glands 215-16
  senses/sensory organs 223-4
  sight 223
  skeletal system 211-12, 213
  skin glands 224
  skull 211, 213-14
  spleen 213
  Steno's gland 213
  stomach 216-17
  tail 210
  thermoregulation 209
  thymus 213
  thyroid gland 222
  touch 224
  urinary system 219
  vibrissae 224
  vomeronasal organ 213
  Zymbal's gland 224
rat clinical notes
  chromodacryorrhea 223
  high frequency sound sensitivity 224
  incisor tooth lengths 210, 214
  mammary tumors 222
  nose breathing 213
  pituitary tumors 222
  sebaceous secretions in older males 224
  sialodacryoadenitis virus (SDAV) 216
  vaginal smears **221**
  venepuncture sites 212
Rattus norvegicus see rat
Rattus rattus (Black rat) 209
reptile anatomy/physiology 17-39
  adrenal glands 34-5, 71
  anaerobiosis 18
  blood cells 25
  blood shunting 24-5
  blood volume 25
  bone structure 21
  calcium/phosphorus 22
  cardiovascular systems 23-5, 48-9, 64, 83-4
  chitin digestion 28
  cloaca 28
  cloacal/colonic absorption 30
  color production 37

reptile anatomy/physiology—*Cont'd*
- dentition 27-8
- dermis 37
- digestive systems 27-9, 51, 66-9, 87-9
- ecdysis/dysecdysis 36-7
- egg structure 34
- egg tooth 28
- endocrine system 34-5
- epidermis 37
- fat bodies 28, 34
- feeding frequency 29
- gastrointestinal tract 28
- growth 22
- hearing 35
- heart, intracardiac blood flow 23-4
- heart rate 25
- hormones 31
- immune system 25-6
- integument 36-8
- iridescence 37
- lower respiratory tract 26
- maternal care 34
- metabolism 18-21
- nervous system 35-6
- osmoregulation 29-31
- oviparity 33
- pancreas 35
- parathyroid glands 34
- pineal gland 35
- renal portal system 31
- reproductive systems 31-4, 52-3, 70-2, 89-91
- respiratory system 26-7
- salt glands 30
- senses/sensory organs 35-6
- sex determination
    - genotype 31
    - temperature-dependence (TSD) 31-2
- sexual maturity 31
- size 17
- skeletal systems 21-3, 43-8, 60-4, 81-3
- skull 22
- taste 35
- taxonomy **18**
- thyroid glands 34
- upper respiratory tract 26
- uric acid 30
- urinary systems 29-31, 52, 69, 89
- ventilation 27
- vertebrae 22-3
- viviparity 34
- water conservation, glomerular filtration rate reduction 30
- *see also named reptile groups*; thermoregulation

reptile clinical notes
- blood shunting 24-5
- blood smears 25
- digestion at low temperatures 29
- drug administration 31
- dysecdysis 36, 37
- fasting pre hibernation 29
- oxygen supply 27
- respiratory surfaces 27
- salt glands 30
- water conservation 30-1
- wound healing 36
- *see also named reptile groups*

rete mirabile, birds 114

Rhynchocephalia 17, 18

rodents
- adaptation to arid environment 167, 229
- coprophagy 168
- dentition and gnawing 169-70

rodents—*Cont'd*
- reproduction 166, 170
- senses/sensory organs 171
- taxonomy **166**, 167-68
- thermoregulation and size 165, 168-9
- *see also* guinea pig; hamster; rat

ruminants, gastrointestinal tract 177

S

salamanders (Caudata) 3, **6**, 7

Salamandra salamandra (Fire salamander) 13

salt glands
- birds 119, 137
- lizards 69
- reptiles 30, 69

Sauria
- taxonomy and classification **18**, **57**
- *see also* lizards

Sauromalus spp. (Chuckwalla) 30, 58

Scincidae 60

Sciuromorpha 166

Serpentes, taxonomy **57**, 77-8

sialodacryoadenitis virus (SDAV), rat 216

Siren spp. 7

skull
- anapsid/diapsid 24
- birds 100-3
- ferret 238, 239, 243
- guinea pig 198, 202
- hamster 230
- Psittaciformes 119
- rabbit 180-2
- rat 211, 213-14
- reptile 22
    - lizard 60-1
    - snake 81-3

snake anatomy/physiology 77-93
- breeding season 90
- cardiovascular system 83-4
- caudal third 80-1
- copulation 90-1
- cranial third 78-80
- dentition 87
- digestive system 87-9
- ecdysis/dysecdysis 36-7, 92-3
- external anatomy 78
- female reproductive system 32-3, 90
- gastrointestinal tract 88-9
- gastropeges 36
- Harderian gland 36
- head structure 36
- integument 92-3
- locomotion 81-3
    - concertina 83
    - lateral undulation 82
    - rectilinear 82
    - sidewinding 83
- lower respiratory tract 86
- male reproductive system 32, 90
- maternal behavior 90
- middle third 80
- opisthoglyphous (rear-fanged) 87-8
- proteroglyphous (front-fanged) 88
- reproductive system 89-91
- respiratory cycle 86-7
- respiratory system 84-7
- senses/sensory organs 91-2
- sexing 90
- sexual maturity 89
- skeletal system 81-3
- skull 81-3
- spurs (pelvic vestiges) 6, 83

snake anatomy/physiology—*Cont'd*
- taxonomy *see* Serpentes
- thermoregulation 78
- tongue 88
- upper respiratory tract 84-6
- urinary system 89
- venom glands 87-8
- vertebrae 81, 84
- *see also* reptiles

snake clinical notes
- failure to shed 92
- incisions 84
- intubation 85
- IPPV 86
- stomach intubation 89
- venepuncture sites 84

Somateria mollisima (Eider) 154

Sphenodon punctatus (tuatara) 17

Squamata, taxonomy and classification 18

Steno's gland 213

Streptococcus zooepidemicus abscessation 200

streptostyly 60

Strigiformes, characteristics **97**

Syrian hamster *see* hamster anatomy/physiology

syrinx 120-1
- in drakes 121

T

temperature-dependent sex determination (TSD), reptiles 31-2

temporalis muscle 165, 166-8

Testudo graeca (Spur-thigh tortoise) 44

Thamnophis sirtalis (Garter snake) 33, 34

thecodont dentition, crocodiles 27-8

thermogenesis 19

thermoregulation
- adaptation to arid environment 138, 167, 229
- behavioral 20, 99
- blood shunting 99
- body mass and shape 20, 99
- body posture 58
- color change 58
- control 19
- ectothermy, advantages/disadvantages 19
- evaporation 99
- heart rate and blood shunting 20
- heliothermic shuttling 58
- heliothermy 20
- in amphibians 5-6
- in birds 99
- in guinea pigs 197
- in hamster 227
- in lizards 58
- in mammals 167, 173
- in rabbit 167, 173
- in rat 209
- in reptiles 19-21
- in snakes 78
- in tortoises and turtles 42
- lighting 20
- mechanisms 20
- plumage 99
- preferred optimal temperature zone (POTZ) 6, 19-20
- thigmothermy 20
- *see also* hibernation

tortoise and turtle anatomy/physiology 41-56
- accessory respiratory organs 51
- cardiovascular system 48-9
    - venepuncture sites 48-9

tortoise and turtle anatomy/physiology—*Cont'd*
  cervical vertebrae 45
  color 48
  copulation 53
  digestive system 51
  ecdysis 48
  female reproductive system 53
  freshwater/marine 42-3
  hibernation 21, 42
  immune system 49
  kidneys 52
  limbs 46-7
  locomotion 43
  longevity 41
  male reproductive system 32, 52-3
  pectoral/pelvic girdles 46
  reproductive system 52-3
  respiratory system 49-50, 52
  scutes 44, 47
  senses/sensory organs 54
  shell 44-8
  shell modifications/patterns 48
  size 41
  skeletal system and integument 43-8
  taxonomy 41, 43
  terrestrial/aquatic 42
  thermoregulation 41-2
  urinary system 52
  ventilation 50-1
    aquatic/terrestrial 51
  vertebrae 44-5
  see also reptiles
tortoise and turtle clinical notes
  age measurement 47
  growth 48
  habitat requirements 20
  intubation 50
  pneumonia 51
  sex differentiation 52
  tympanic squamous metaplasia 55
  weight loss in hibernation 21
  see also reptile clinical notes
Trachemys see Pseudemys
Trichobezoars, rabbits 181
Trichobatrachus spp. (African hairy frogs) 9
tubocurare 36
turtles *see* tortoise and turtle

U

uterus, placental mammals 164

V

Varanidae 60
Varanus exanthematicus (Bosc monitor) 19, 60
Varanus gouldii (Australian sand monitor) 66
Varanus komodoensis (Komodo dragon) 60
venepuncture sites
  amphibians 8, 9
  birds 115-16
  ferret 239, 240
  guinea pig 199
  hamster 228
  lizards 64
  rat 212
  snakes 84
  tortoise and turtle 48-9
vibrissae 208, 224
Viperidae 77-8
vitamin A, psittacines 129
vitamin C, guinea pig 201
vitamin D, rabbit 189-90
viviparity 34, 72

W

water conservation, reptiles 30-1
waterfowl
  beak and tongue 127, 149
  diving cardiac physiology 116
wing drop: coracoid fracture 106
wings 105-7, **108**, 152-3

X

Xenopus laevis (Clawed frog) 10

Z

zygodactyly 112
Zymbal's gland 223